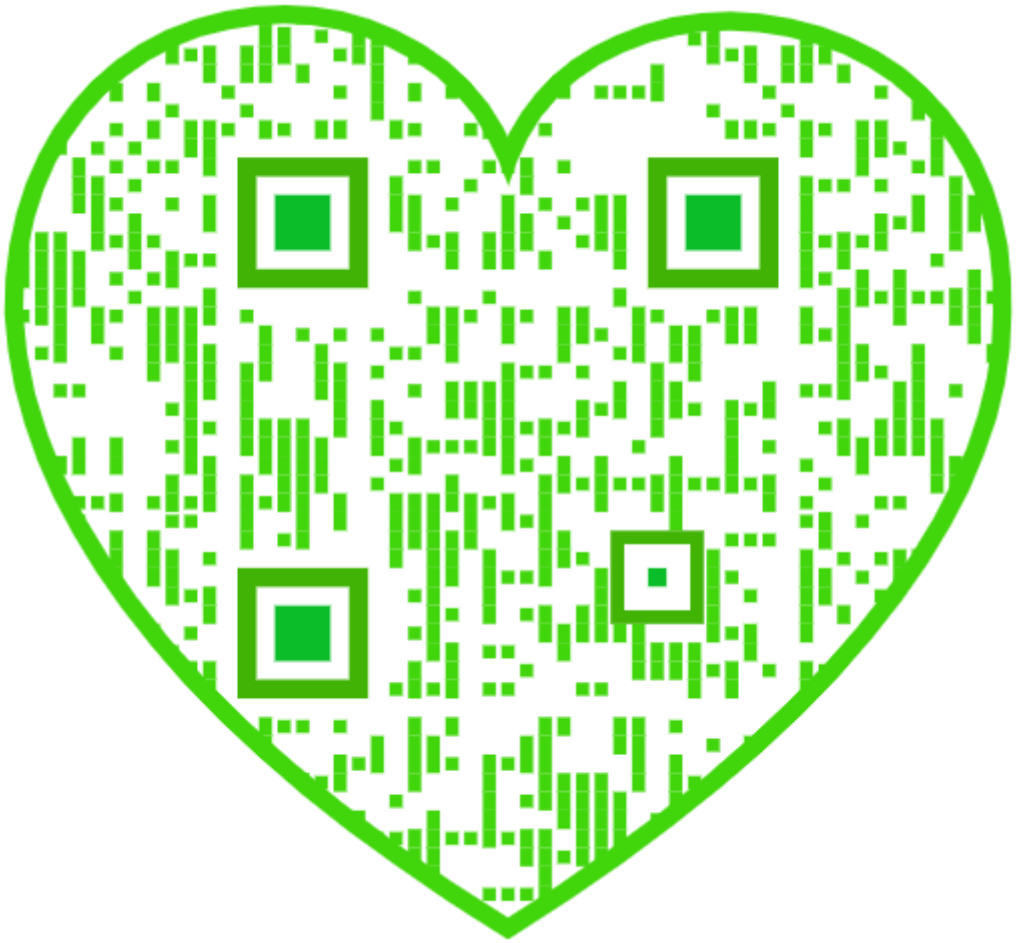

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TWENTIETH CENTURY TEXT-BOOKS

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TWENTIETH CENTURY TEXT-BOOKS

PLANT STRUCTURES

A SECOND BOOK OF BOTANY

BY

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PREFACE

In the preface to *Plant Relations* the author gave his reasons for suggesting that the ecological standpoint is best adapted for the first contact with plants. It may be, however, that many teachers will prefer to begin with the morphological standpoint, as given in the present book. Recognizing this fact, *Plant Structures* has been made an independent volume that may precede or follow the other, or may provide a brief course of botanical study in itself.

Although in the present volume Morphology is the dominant subject, it seems wise to give a somewhat general view of plants, and therefore Physiology, Ecology, and Taxonomy are included in a general way. For fear that Physiology and Ecology may be lost sight of as distinct subjects, and to introduce important topics not included in the body of the work, short chapters are devoted to them, which seek to bring together the main facts, and to call attention to the larger fields.

This book is not a laboratory guide, but is for reading and study in connection with *laboratory work*. An accompanying pamphlet for teachers gives helpful suggestions to those who are not already familiar with its scope and purpose. It is not expected that all the forms and subjects presented in the text can be included in the *laboratory exercises*, but it is believed that the book will prove a useful companion in connection with such exercises. It is very necessary to co-ordinate the results of *laboratory work*, to refer to a larger range of material than can be handled, and to develop some philosophical conception of

the plant kingdom. The learning of methods and the collection of facts are fundamental processes, but they must be supplemented by information and ideas to be of most service.

The author does not believe in the use of technical terms unless absolutely necessary, for they lead frequently to mistaking definitions of words for knowledge of things. But it is necessary to introduce the student not merely to the main facts but also to the literature of botany. Accordingly, the most commonly used technical terms are introduced, often two or three for the same thing, but it is hoped that familiarity with them will enable the student to read any ordinary botanical text. Care has been taken to give definitions and derivations, and to call repeated attention to synonymous terms, so that there may be no confusion. The chaotic state of morphological terminology tempted the author to formulate or accept some consistent scheme of terms; but it was felt that this would impose upon the student too great difficulty in reading far more important current texts.

Chapters I–XII form a connected whole, presenting the general story of the evolution of plants from the lowest to the highest. The remaining chapters are supplementary, and can be used as time or inclination permits, but it is the judgment of the author that they should be included if possible. The flower is so conspicuous and important a feature in connection with the highest plants, that Chapter XIII seems to be a fitting sequel to the preceding chapters. It also seems desirable to develop some knowledge of the great Angiosperm families, as presented in Chapter XIV, since they are the most conspicuous members of every flora. In this connection, the author has been in the habit of directing the examination of characteristic flowers, and of teaching the use of ordinary taxonomic manuals. Chapter XV deals with anatomical matters, but the structures included are so bound up with the form and work of plants

that it seems important to find a place for them even in an elementary work. The reason for Chapters XVI and XVII has been stated already, and even if *Plant Relations* is studied, Chapter XVII will be useful either as a review or as an introduction. In the chapter on Plant Physiology the author has been guided by Noll's excellent *résumé* in the "Strasburger" Botany.

The illustrations have been entirely in the charge of Dr. Otis W. Caldwell, who for several years has conducted in the University, and in a most efficient way, such laboratory work as this volume implies. Many original illustrations have been prepared by Dr. Caldwell and his assistants, and some are credited to Dr. Chamberlain and Dr. Cowles, of the University, but it is a matter of regret that pressure of work and time limitation have forbidden a still greater number. The authors of the original illustrations are cited, and where illustrations have been obtained elsewhere the sources are indicated. The descriptions given in connection with each illustration are unusually full, and should be studied carefully, as frequently they contain important material not included in the text.

The author would again call attention to the fact that this book is merely intended to serve as a compact supplement to three far more important factors: the teacher, the laboratory, and field work. Without these it can not serve its purpose.

JOHN M. COULTER.

THE UNIVERSITY OF CHICAGO, *November*, 1899.

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BOTANY

PART II.—PLANT STRUCTURES

CHAPTER I

INTRODUCTION

1. **Differences in structure.**—It is evident, even to the casual observer, that plants differ very much in structure. They differ not merely in form and size, but also in complexity. Some plants are simple, others are complex, and the former are regarded as of lower rank.

Beginning with the simplest plants—that is, those of lowest rank—one can pass by almost insensible gradations to those of highest rank. At certain points in this advance notable interruptions of the continuity are discovered, structures, and hence certain habits of work, changing decidedly, and these breaks enable one to organize the vast array of plants into groups. Some of the breaks appear to be more important than others, and opinions may differ as to those of chief importance, but it is customary to select three of them as indicating the division of the plant kingdom into four great groups.

2. **The great groups.**—The four great groups may be indicated here, but it must be remembered that their names mean nothing until plants representing them have been studied. It will be noticed that all the names have the

constant termination *phytes*, which is a Greek word meaning "plants." The prefix in each case is also a Greek word intended to indicate the kind of plants.

(1) *Thallophytes.*—The name means "thallus plants," but just what a "thallus" is can not well be explained until some of the plants have been examined. In this great group are included some of the simplest forms, known as *Algæ* and *Fungi*, the former represented by green thready growths in fresh water and the great host of seaweeds, the latter by moulds, mushrooms, etc.

(2) *Bryophytes.*—The name means "moss plants," and suggests very definitely the forms which are included. Every one knows mosses in a general way, but associated with them in this great group are the allied liverworts, which are very common but not so generally known.

(3) *Pteridophytes.*—The name means "fern plants," and ferns are well known. Not all Pteridophytes, however, are ferns, for associated with them are the horsetails (scouring rushes) and the club mosses.

(4) *Spermatophytes.*—The name means "seed plants"—that is, those plants which produce seeds. In a general way these are the most familiar plants, and are commonly spoken of as "flowering plants." They are the highest in rank and the most conspicuous, and hence have received much attention. In former times the study of botany in the schools was restricted to the examination of this one group, to the entire neglect of the other three great groups.

3. **Increasing complexity.**—At the very outset it is well to remember that the Thallophytes contain the simplest plants—those whose bodies have developed no organs for special work, and that as one advances through higher Thallophytes, Bryophytes, and Pteridophytes, there is a constant increase in the complexity of the plant body, until in the Spermatophytes it becomes most highly organized, with numerous structures set apart for special work. just as in the highest animals limbs, eyes, ears, bones, muscles, nerves, etc.,

are set apart for special work. The increasing complexity is usually spoken of as *differentiation*—that is, the setting apart of structures for different kinds of work. Hence the Bryophytes are said to be more highly differentiated than the Thallophytes, and the Spermatophytes are regarded as the most highly differentiated group of plants.

4. **Nutrition and reproduction.**—However variable plants may be in complexity, they all do the same general kind of work. Increasing complexity simply means an attempt to do this work more effectively. It is plant work that makes plant structures significant, and hence in this book no attempt will be made to separate them. All the work of plants may be put under two heads, *nutrition* and *reproduction*, the former including all those processes by which a plant maintains itself, the latter those processes by which it produces new plants. In the lowest plants, these two great kinds of work, or *functions*, as they are called, are not set apart in different regions of the body, but usually the first step toward differentiation is to set apart the reproductive function from the nutritive, and to develop special reproductive organs which are entirely distinct from the general nutritive body.

5. **The evolution of plants.**—It is generally supposed that the more complex plants have descended from the simpler ones; that the Bryophytes have been derived from the Thallophytes, and so on. All the groups, therefore, are supposed to be related among themselves in some way, and it is one of the great problems of botany to discover these relationships. This theory of the relationship of plant groups is known as the *theory of descent*, or more generally as *evolution*. To understand any higher group one must study the lower ones related to it, and therefore the attempt of this book will be to trace the evolution of the plant kingdom, by beginning with the simplest forms and noting the gradual increase in complexity until the highest forms are reached.

CHAPTER II

THALLOPHYTES: ALGÆ

6. **General characters.**—Thallophytes are the simplest of plants, often so small as to escape general observation, but sometimes with large bodies. They occur everywhere in large numbers, and are of special interest as representing the beginnings of the plant kingdom. In this group also there are organized all of the principal activities of plants, so that a study of Thallophytes furnishes a clew to the structures and functions of the higher, more complex groups.

The word "thallus" refers to the nutritive body, or vegetative body, as it is often called. This body does not differentiate special nutritive organs, such as the leaves and roots of higher plants, but all of its regions are alike. Its natural position also is not erect, but prone. While most Thallophytes have thallus bodies, in some of them, as in certain marine forms, the nutritive body differentiates into regions which resemble leaves, stems, and roots ; also certain Bryophytes have thallus bodies. The thallus body, therefore, is not always a distinctive mark of Thallophytes, but must be supplemented by other characters to determine the group.

7. **Algæ and Fungi.**—It is convenient to separate Thallophytes into two great divisions, known as *Algæ* and *Fungi*. It should be known that this is a very general division and not a technical one, for there are groups of Thallophytes which can not be regarded as strictly either Algæ or Fungi, but for the present these groups may be included.

The great distinction between these two divisions of Thallophytes is that the Algæ contain *chlorophyll* and the Fungi do not. Chlorophyll is the characteristic green coloring matter found in plants, the word meaning "leaf green." It may be thought that to use this coloring material as the basis of such an important division is somewhat superficial, but it should be known that the presence of chlorophyll gives a peculiar power—one which affects the whole structure of the nutritive body and the habit of life. The presence of chlorophyll means that the plant can make its own food, can live independent of other plants and animals. Algæ, therefore, are the independent Thallophytes, so far as their food is concerned, for they can manufacture it out of the inorganic materials about them.

The Fungi, on the other hand, contain no chlorophyll, can not manufacture food from inorganic material, and hence must obtain it already manufactured by plants or animals. In this sense they are dependent upon other organisms, and this dependence has led to great changes in structure and habit of life.

It is supposed that Fungi have descended from Algæ—that is, that they were once Algæ, which gradually acquired the habit of obtaining food already manufactured, lost their chlorophyll, and became absolutely dependent and more or less modified in structure. Fungi may be regarded, therefore, as reduced relatives of the Algæ, of equal rank so far as birth and structure go, but of very different habits.

ALGÆ

8. **General characters.**—As already defined, Algæ are Thallophytes which contain chlorophyll, and are therefore able to manufacture food from inorganic material. They are known in general as "seaweeds," although there are fresh-water forms as well as marine. They are exceedingly variable in size, ranging from forms visible only by means

of the compound microscope to marine forms with enormously bulky bodies. In general they are *hydrophytes*—that is, plants adapted to life in water or in very moist places. The special interest connected with the group is that it is supposed to be the ancestral group of the plant kingdom—the one from which the higher groups have been more or less directly derived. In this regard they differ from the Fungi, which are not supposed to be responsible for any higher groups.

9. **The subdivisions.**—Although all the Algæ contain chlorophyll, some of them do not appear green. In some of them another coloring matter is associated with the chlorophyll and may mask it entirely. Advantage is taken of these color associations to separate Algæ into subdivisions. As these colors are accompanied by constant differences in structure and work, the distinction on the basis of colors is more real than it might appear. Upon this basis four subdivisions may be made. The constant termination *phyceæ*, which appears in the names, is a Greek word meaning "seaweed," which is the common name for Algæ; while the prefix in each case is the Greek name for the color which characterizes the group.

The four subdivisions are as follows: (1) *Cyanophyceæ*, or "Blue Algæ," but usually called "Blue-green Algæ," as the characteristic blue does not entirely mask the green, and the general tint is bluish-green; (2) *Chlorophyceæ*, or "Green Algæ," in which there is no special coloring matter associated with the chlorophyll; (3) *Phæophyceæ*, or "Brown Algæ"; and (4) *Rhodophyceæ*, or "Red Algæ."

It should be remarked that probably the Cyanophyceæ do not belong with the other groups, but it is convenient to present them in this connection.

10. **The plant body.**—By this phrase is meant the nutritive or vegetative body. There is in plants a unit of structure known as the *cell*. The bodies of the simplest plants consist of but one cell, while the bodies of the most com-

plex plants consist of very many cells. It is necessary to know something of the ordinary living plant cell before the bodies of Algæ or any other plant bodies can be understood.

Such a cell if free is approximately spherical in outline, (Fig. 6), but if pressed upon by contiguous cells may become variously modified in form (Fig. 1). Bounding it there is a thin, elastic wall, composed of a substance called *cellulose*. The cell wall, therefore, forms a delicate sac, which contains the living substance known as *protoplasm*. This is the substance which manifests life, and is the only substance in the plant which is alive. It is the protoplasm which has organized the cellulose wall about itself, and which does all the plant work. It is a fluid substance which varies much in its consistence, sometimes being a thin viscous fluid, like the white of an egg, sometimes much more dense and compactly organized.

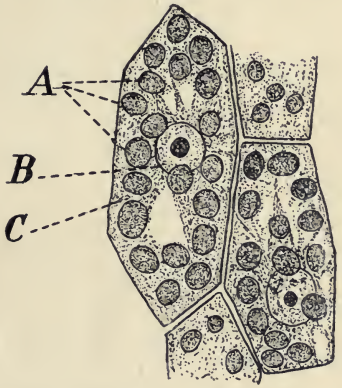


Fig. 1. Cells from a moss leaf, showing nucleus (*B*) in which there is a nucleolus, cytoplasm (*C*), and chloroplasts (*A*).—Caldwell.

The protoplasm of the cell is organized into various structures which are called *organs of the cell*, each organ having one or more special functions. One of the most conspicuous organs of the living cell is the single *nucleus*, a comparatively compact and usually spherical protoplasmic body, and generally centrally placed within the cell (Fig. 1). All about the nucleus, and filling up the general cavity within the cell wall, is an organized mass of much thinner protoplasm, known as *cytoplasm*. The cytoplasm seems to form the general background or matrix of the cell, and the

nucleus lies imbedded within it (Fig. 1). Every working cell consists of at least cytoplasm and nucleus. Sometimes the cellulose wall is absent, and the cell then consists simply of a nucleus with more or less cytoplasm organized about it, and is said to be *naked*.

Another protoplasmic organ of the cell, very conspicuous among the Algæ and other groups, is the *plastid*. Plastids are relatively compact bodies, commonly spherical, variable in number, and lie imbedded in the cytoplasm. There are various kinds of plastids, the most common being the one which contains the chlorophyll and hence is stained green. The chlorophyll-containing plastid is known as the *chloroplastid*, or *chloroplast* (Fig. 1). An ordinary alga-cell, therefore, consists of a cell wall, within which the protoplasm is organized into cytoplasm, nucleus, and chloroplasts.

The bodies of the simplest Algæ consist of one such cell, and it may be regarded as the simplest form of plant body. Starting with such forms, one direction of advance in complexity is to organize several such cells into a loose row, which resembles a chain (Fig. 4); in other forms the cells in a row become more compacted and flattened, forming a simple *filament* (Figs. 2, 5); in still other forms the original filament puts out branches like itself, producing a branching filament (Fig. 8). These *filamentous* bodies are very characteristic of the Algæ.

Starting again with the one-celled body, another line of advance is for several cells to organize in two directions, forming a *plate* of cells. Still another line of advance is for the cells to organize in three directions, forming a *mass* of cells.

The bodies of Algæ, therefore, may be said to be one-celled in the simplest forms, and in the most complex forms they become filaments, plates, or masses of cells.

11. **Reproduction.**—In addition to the work of nutrition, the plant body must organize for reproduction. Just as the nutritive body begins in the lowest forms with a single cell

and becomes more complex in the higher forms, so reproduction begins in very simple fashion and gradually becomes more complex. Two general types of reproduction are employed by the Algæ, and all other plants. They are as follows:

(1) *Vegetative multiplication.*—This is the only type of reproduction employed by the lowest Algæ, but it persists in all higher groups even when the other method has been introduced. In this type no special reproductive bodies are formed, but the ordinary vegetative body is used for the purpose. For example, if the body consists of one cell, that cell cuts itself into two, each half grows and rounds off as a distinct cell, and two new bodies appear where there was one before (Figs. 3, 6). This process of cell division is very complicated and important, involving a division of nucleus and cytoplasm so that the new cells may be organized just as was the old one. Wherever ordinary nutritive cells are used directly to produce new plant bodies the process is *vegetative multiplication.* This method of reproduction may be indicated by a formula as follows: P—P—P—P—P, in which P stands for the plant, the formula indicating that a succession of plants may arise directly from one another without the interposition of any special structure.

(2) *Spores.*—Spores are cells which are specially organized to reproduce, and are not at all concerned in the nutritive work of the plant. Spores are all alike in their power of reproduction, but they are formed in two very distinct ways. It must be remembered that these two types of spores are alike in power but different in origin.

Asexual spores.—These cells are formed by cell division. A cell of the plant body is selected for the purpose, and usually its contents divide and form a variable number of new cells within the old one (Fig. 2, *B*). These new cells are *asexual spores*, and the cell which has formed them within itself is known as the *mother cell.* This peculiar kind of cell division, which does not involve the wall of the

old cell, is often called *internal division*, to distinguish it from *fission*, which involves the wall of the old cell, and is the ordinary method of cell division in nutritive cells.

If the mother cell which produces the spores is different from the other cells of the plant body it is called the *sporangium*, which means "spore vessel." Often a cell is nutritive for a time and afterward becomes a mother cell, in which case it is said to function as a sporangium. The wall of a sporangium usually opens, and the spores are discharged, thus being free to produce new plants. Various names have been given to asexual spores to indicate certain peculiarities. As Algæ are mostly surrounded by water, the characteristic asexual spore in the group is one that can swim by means of minute hair-like processes or *cilia*, which have the power of lashing the water (Fig. 7, *C*). These ciliated spores are known as *zoospores*, or "animal-like spores," referring to their power of locomotion; sometimes they are called *swimming spores*, or *swarm spores*. It must be remembered that all of these terms refer to the same thing, a swimming asexual spore.

This method of reproduction may be indicated by a formula as follows: P — o — P — o — P — o — P, which indicates that new plants are not produced directly from the old ones, as in vegetative multiplication, but that between the successive generations there is the asexual spore.

Sexual spores.—These cells are formed by cell union, two cells fusing together to form the spore. This process of forming a spore by the fusion of two cells is called the *sexual process*, and the two special cells (sexual cells) thus used are known as *gametes* (Fig. 2, *C*, *d*, *e*). It must be noticed that gametes are not spores, for they are not able alone to produce a new plant; it is only after two of them have fused and formed a new cell, the spore, that a plant can be produced. The spore thus formed does not differ in its power from the asexual spore, but it differs very much in its method of origin.

The gametes are organized within a mother cell, and if this cell is distinct from the other cells of the plant it is called a *gametangium*, which means "gamete vessel."

This method of reproduction may be indicated by a formula as follows: $P = \overset{\circ}{\circ} > o - P = \overset{\circ}{\circ} > o - P = \overset{\circ}{\circ} > o - P$, which indicates that two special cells (gametes) are produced by the plant, that these two fuse to form one (sexual spore), which then produces a new plant.

It must not be supposed that if a plant uses one of these three methods of reproduction (vegetative multiplication, asexual spores, sexual spores) it does not employ the other two. All three methods may be employed by the same plant, so that new plants may arise from it in three different ways.

CHAPTER III

THE EVOLUTION OF SEX

12. **The general problem.**—In the last chapter it was remarked that the simplest Algæ reproduce only by vegetative multiplication, the ordinary cell division (fission) of nutritive cells multiplying cells and hence individuals. Among other low Algæ asexual spores are added to fission as a method of reproduction, the spores being also formed by cell division, generally internal division. In higher forms gametes appear, and a new method of reproduction, the sexual, is added to the other two.

Sexual reproduction is so important a process in all plants except the lowest, that it is of interest to discover how it may have originated, and how it developed into its highest form. Among the Algæ the origin and development of the sexual process seems to be plainly suggested; and as all other plant groups have probably been derived more or less directly from Algæ, what has been accomplished for the sexual process in this lowest group was probably done for the whole plant kingdom.

13. **The origin of gametes.**—One of the best Algæ to illustrate the possible origin of gametes is a common freshwater form known as *Ulothrix* (Fig. 2). The body consists of a simple filament composed of a single row of short cells (Fig. 2, *A*). Each cell contains a nucleus, and a single large chloroplast which has the form of a thick cylinder investing the rest of the cell contents. Through the microscope, if the focus is upon the center of the cell, an optical section of the cylinder is obtained, the chloro-

plast appearing as a thick green mass on each side of the central nucleus. As no other color appears, it is evident that *Ulothrix* is one of the Chlorophyceæ.

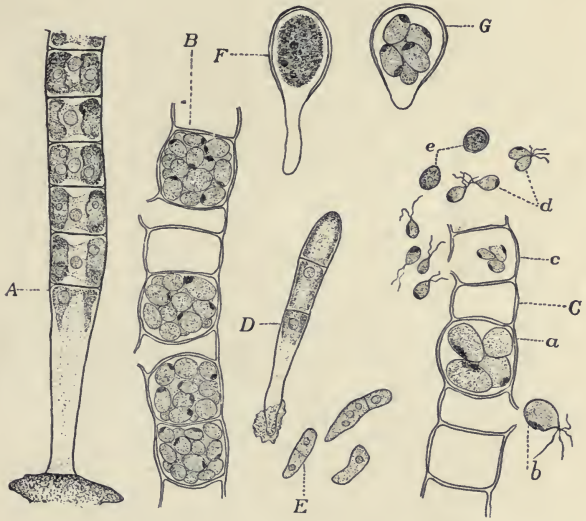


FIG. 2. *Ulothrix*, a Conferva form. *A*, base of filament, showing lowest holdfast cell and five vegetative cells, each with its single conspicuous cylindrical chloroplast (seen in section) inclosing a nucleus; *B*, four cells containing numerous small zoospores, the others emptied; *C*, fragment of a filament showing one cell (*a*) containing four zoospores, another zoospore (*b*) displaying four cilia at its pointed end and just having escaped from its cell, another cell (*c*) from which most of the small biciliate gametes have escaped, gametes pairing (*d*), and the resulting zygotes (*e*); *D*, beginning of new filament from zoospore; *E*, feeble filaments formed by the small zoospores; *F*, zygote growing after rest; *G*, zoospores produced by zygote.—CALDWELL, except *F* and *G*, which are after DODEL-PORT.

The cells are all alike, excepting that the lowest one of the filament is mostly colorless, and is elongated and more or less modified to act as a holdfast, anchoring the filament to some firm support. With this exception the cells are all nutritive; but any one of them has the power of organizing for reproduction. This indicates that at first nutritive and

reproductive cells are not distinctly differentiated, but that the same cell may be nutritive at one time and reproductive at another.

In suitable conditions certain cells of the filament will be observed organizing within themselves new calls by internal division (Fig. 2, *C*, *a*, *b*). The method of formation at once suggests that the new cells are asexual spores, and the mother cell which produces them is acting as a sporangium. The spores escape into the water through an opening formed in the wall of the mother cell, and each is observed to have four cilia at the pointed end, by means of which it swims, and hence it is a zoospore or swarm spore. After swimming about for a time, the zoospores "settle down," lose their cilia, and begin to develop a new filament like that from which they came (Fig. 2, *D*).

Other cells of the same filament also act as mother cells, but the cells which they produce are more numerous, hence smaller in size than the zoospores, and they have but two cilia (Fig. 2, *C*, *c*). They also escape into the water and swim about, except in size and in number of cilia resembling the zoospores. In general they seem to be unable to act as the zoospores in the formation of new filaments, but occasionally one of them forms a filament much smaller than the ordinary one (Fig. 2, *E*). This indicates that they may be zoospores reduced in size, and unable to act as the larger ones. The important fact, however, is that these smaller swimming cells come together in pairs, each pair fusing into one cell (Fig. 2, *C*, *d*, *e*). The cells thus formed have the power of producing new filaments more or less directly.

It is evident that this is a sexual act, that the cell produced by fusion is a sexual spore, that the two cells which fuse are gametes, and that the mother cell which produces them acts as a gametangium. Cases of this kind suggest that the gametes or sex cells have been derived from zoospores, and that asexual spores have given rise to sex cells.

The appearance of sex cells (gametes) is but one step in the evolution of sex. It represents the attainment of sexuality, but the process becomes much more highly developed.

14. **Isogamy.**—When gametes first appear, in some such way as has been described, the two which fuse seem to be exactly alike. They resemble each other in size and activity, and in every structure which can be distinguished. This fact is indicated by the word *isogamy*, which means "similar gametes," and those plants whose pairing gametes are similar, as *Ulothrix*, are said to be *isogamous*.

The act of fusing of similar gametes is usually called *conjugation*, which means a "yoking together" of similar bodies. Of course it is a sexual process, but the name is convenient as indicating not merely the process, but also an important character of the gametes. The sexual spore which results from this act of conjugation is called the *zygote* or *zygospore*, meaning "yoked spore."

In isogamy it is evident that while sexuality has been attained there is no distinction between sexes, as obtains in the higher plants. It may be called a *unisexual* condition, as opposed to a *bisexual* one. The next problem in the evolution of sex, therefore, is to discover how a bisexual condition has been derived from a unisexual or isogamous one.

15. **Heterogamy.**—Beginning with isogamous forms, a series of plants can be selected illustrating how the pairing gametes gradually became unlike. One of them becomes less active and larger, until finally it is entirely passive and very many times larger than its mate (Fig. 7). The other retains its small size and increases in activity. The pairing gametes thus become very much differentiated, the larger passive one being the *female* gamete, the smaller active one the *male* gamete. This condition is indicated by the word *heterogamy*, which means "dissimilar gametes," and those plants whose pairing gametes are dissimilar are said to be *heterogamous*.

In order to distinguish them the large and passive female gamete is called the *oosphere*, which means "egg sphere," or it is called the *egg;* the small but active male gamete is variously called the *spermatozoid*, the *antherozoid*, or simply the *sperm*. In this book egg and sperm will be used, the names of similar structures in animals.

In isogamous plants the mother cells (gametangia) which produce the gametes are alike; but in heterogamous plants the gametes are so unlike that the gametangia which produce them become unlike. Accordingly they have received distinctive names, the gametangium which produces the sperms being called the *antheridium*, that producing the egg being called the *oogonium* (Fig. 10).

The act of fusing of sperm and egg is called *fertilization*, which is the common form of the sexual process. The sexual spore which results from fertilization is known as the *oospore* or "egg-spore," sometimes called the *fertilized egg*.

It is evident that heterogamous plants are bisexual, and bisexuality is not only attained among Algæ, but it prevails among all higher plants. Among the lowest forms there is only vegetative multiplication; higher forms added sexuality; then still higher forms became bisexual.

16. **Summary.**—Isogamous forms produce gametangia, which produce similar gametes, which by conjugation form zygotes. Heterogamous forms produce antheridia and oogonia, which produce sperms and eggs, which by fertilization form oospores.

CHAPTER IV

THE GREAT GROUPS OF ALGÆ

17. **General characters.**—The Algæ are distinguished among Thallophytes by the presence of chlorophyll. It was stated in a previous chapter that in three of the four great groups another coloring matter is associated with the chlorophyll, and that this fact is made the basis of a division into Blue-green Algæ (Cyanophyceæ), Green Algæ (Chlorophyceæ), Brown Algæ (Phæophyceæ), and Red Algæ (Rhodophyceæ). In our limited space it will be impossible to do more than mention a few representatives of each group, but they will serve to illustrate the prominent facts.

1. Cyanophyceæ (*Blue-green Algæ*)

18. **Glœocapsa.**—These forms may be found forming blue-green or olive-green patches on damp tree-trunks, rock, walls, etc. By means of the microscope these patches are seen to be composed of multitudes of spherical cells, each representing a complete *Glœocapsa* body. One of the peculiarities of the body is that the cell wall becomes mucilaginous, swells, and forms a jelly-like matrix about the working cell. Each cell divides in the ordinary way, two new *Glœocapsa* individuals being formed, this method of vegetative multiplication being the only form of reproduction (Fig. 3).

When new cells are formed in this way the swollen mucilaginous walls are apt to hold them together, so that presently a number of cells or individuals are found lying

together imbedded in the jelly-like matrix formed by the wall material (Fig. 3). These imbedded groups of individuals are spoken of as *colonies*, and as colonies become large they break up into new colonies, the individual cells composing them continuing to divide and form new individuals. This represents a very simple life history, in fact a simpler one could hardly be imagined.

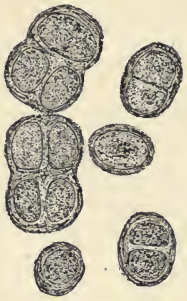


FIG. 3. *Glœocapsa*, a blue-green alga, showing single cells, and small groups which have been formed by division and are held together by the enveloping mucilage.—CALDWELL.

19. **Nostoc.**—These forms occur in jelly-like masses in damp places. If the jelly be examined it will be found to contain imbedded in it numerous cells like those of *Glœocapsa*, but they are strung together to form chains of varying lengths (Fig. 4). The jelly in which these chains are imbedded is the same as that found in *Glœocapsa*, being formed by the cell walls becoming mucilaginous and swollen.

One notable fact is that all the cells in the chain are not alike, for at irregular intervals there occur larger colorless cells, an illustration of the differentiation of cells. These larger cells are known as *heterocysts* (Fig. 4, *A*), which simply means "other cells." It is observed that when the chain breaks up into fragments each fragment is composed of the cells between

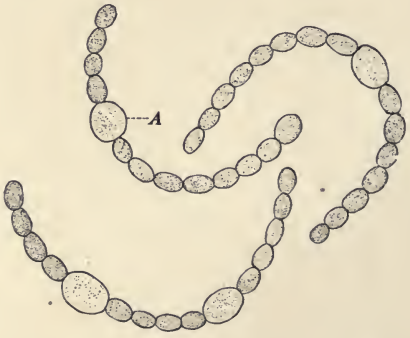


FIG. 4. *Nostoc*, a blue-green alga, showing the chain-like filaments, and the heterocysts (*A*) which determine the breaking up of the chain. —CALDWELL.

two heterocysts. The fragments wriggle out of the jelly matrix and start new colonies of chains, each cell dividing to increase the length of the chain. This cell division, to form new cells, is the characteristic method of reproduction.

At the approach of unfavorable conditions certain cells of the chain become thick-walled and well-protected. These cells which endure the cold or other hardships, and upon the return of favorable conditions produce new chains of cells, are often called spores, but they are better called "resting cells."

20. **Oscillaria.**—These forms are found as bluish-green slippery masses on wet rocks, or on damp soil, or freely floating. They are simple filaments, composed of very short flattened cells (Fig. 5), and the name *Oscillaria* refers to the fact that they exhibit a peculiar oscillating movement. These motile filaments are isolated, not being held together in a jelly-like matrix as are the chains of *Nostoc*, but the wall develops a certain amount of mucilage, which gives the slippery feeling and sometimes forms a thin mucilaginous sheath about the row of cells.

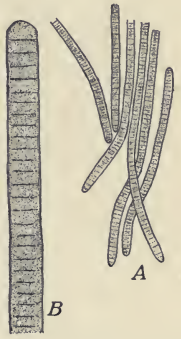


FIG. 5. *Oscillaria*, a blue-green alga, showing a group of filaments (*A*), and a single filament more enlarged (*B*).—CALDWELL.

The cells of a filament are all alike, except that the terminal cell has its free surface rounded. If a filament breaks, and a new cell surface exposed, it at once becomes rounded. If a single cell of the filament is freed from all the rest, both flattened ends become rounded, and the cell becomes spherical or nearly so. These facts indicate at least two important things: (1) that the cell wall is elastic, so that it can be made to change its form, and (2) that it is pressed upon from within, so that if free

it will bulge outward. In all active living cells there is this pressure upon the wall from within.

Each cell of the *Oscillaria* filament has the power of dividing, thus forming new cells and elongating the filament. A filament may break up into fragments of varying lengths, and each fragment by cell division organizes a new filament. Here again reproduction is by means of vegetative multiplication.

21. **Conclusions.**—Taking *Glœocapsa*, *Nostoc*, and *Oscillaria* as representatives of the group Cyanophyceæ, or "green slimes," we may come to some conclusions concerning the group in general. The plant body is very simple, consisting of single cells, or chains and filaments of cells. Although in *Nostoc* and *Oscillaria* the cells are organized into chains and filaments, each cell seems to be able to live and act independently, and the chain and filament seem to be little more than colonies of individual cells. In this sense, all of these plants may be regarded as one-celled.

Differentiation is exhibited in the appearance of heterocysts in *Nostoc*, peculiar cells which seem to be connected in some way with the breaking up of filamentous colonies, although the *Oscillaria* filament breaks up without them.

The power of motion is also well exhibited by the group, the free filaments of *Oscillaria* moving almost continually, and the imbedded chains of *Nostoc* at times moving to escape from the restraining mucilage.

The whole group also shows a strong tendency in the cell-wall material to become converted into mucilage and much swollen, a tendency which reaches an extreme expression in such forms as *Nostoc* and *Glœocapsa*.

Another distinguishing mark is that reproduction is exclusively by means of vegetative multiplication, through ordinary cell division or fission, which takes place very freely. Individual cells are organized with heavy resistant walls to enable them to endure the winter or other unfavorable conditions, and to start a new series of individuals

upon the return of favorable conditions. These may be regarded as resting cells. So notable is the fact of reproduction by fission that Cyanophyceæ are often separated from the other groups of Algæ and spoken of as "Fission Algæ," which put in technical form becomes Schizophyceæ. In this particular, and in several others mentioned above, they resemble the "Fission Fungi" (Schizomycetes), commonly called "bacteria," so closely that they are often associated with them in a common group called "Fission plants" (Schizophytes), distinct from the ordinary Algæ and Fungi.

2. Chlorophyceæ (*Green Algæ*).

22. **Pleurococcus.**—This may be taken as a type of one-celled Green Algæ. It is most commonly found in masses covering damp tree-trunks, etc., and looking like a green stain. These finely granular green masses are found to be made up of multitudes of spherical cells resembling those of *Glœocapsa*, except that there is no blue with the chlorophyll, and the cells are not imbedded in such jelly-like masses. The cells may be solitary, or may cling together in colonies of various sizes (Fig. 6). Like *Glœocapsa*, a cell divides and forms two new cells, the only reproduction

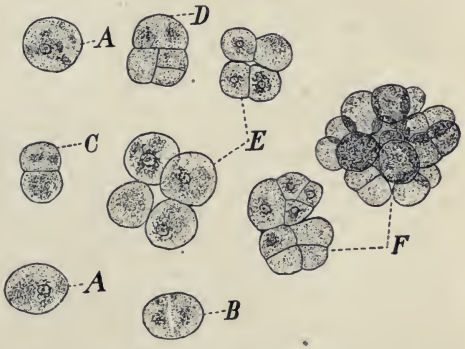


Fig. 6. *Pleurococcus*, a one-celled green alga: *A*, showing the adult form with its nucleus; *B*, *C*, *D*, *E*, various stages of division (fission) in producing new cells; *F*, colonies of cells which have remained in contact.—Caldwell.

being of this simple kind. It is evident, therefore, that the group Chlorophyceæ begins with forms just as simple as are to be found among the Cyanophyceæ.

Pleurococcus is used to represent the group of Protococcus forms, one-celled forms which constitute one of the subdivisions of the Green Algæ. It should be said that *Pleurococcus* is possibly not a Protococcus form, but may be a reduced member of some higher group; but it is so common, and represents so well a typical one-celled green alga, that it is used in this connection. It should be known, also, that while the simplest Protococcus forms reproduce only by fission, others add to this the other methods of reproduction.

23. **Ulothrix.**—This form was described in § 13. It is very common in fresh waters, being recognized easily by its simple filaments composed of short squarish cells, each cell containing a single conspicuous cylindrical chloroplast (Fig. 2). This plant uses cell division to multiply the cells of a filament, and to develop new filaments from fragments of old ones; but it also produces asexual spores in the form of zoospores, and gametes which conjugate and form zygotes. Both zoospores and zygotes have the power of germination—that is, the power to begin the development of a new plant. In the germination of the zygote a new filament is not produced directly, but there are formed within it zoospores, each of which produces a new filament (Fig. 2, *F*, *G*). All three kinds of reproduction are represented, therefore, but the sexual method is the low type called isogamy, the pairing gametes being alike.

Ulothrix is taken as a representative of the Conferva forms, the most characteristic group of Chlorophyceæ. All the Conferva forms, however, are not isogamous, as will be illustrated by the next example.

24. **Edogonium.**—This is a very common green alga, found in fresh waters (Fig. 7). The filaments are long and simple, the lowest cell acting as a holdfast, as in *Ulothrix*

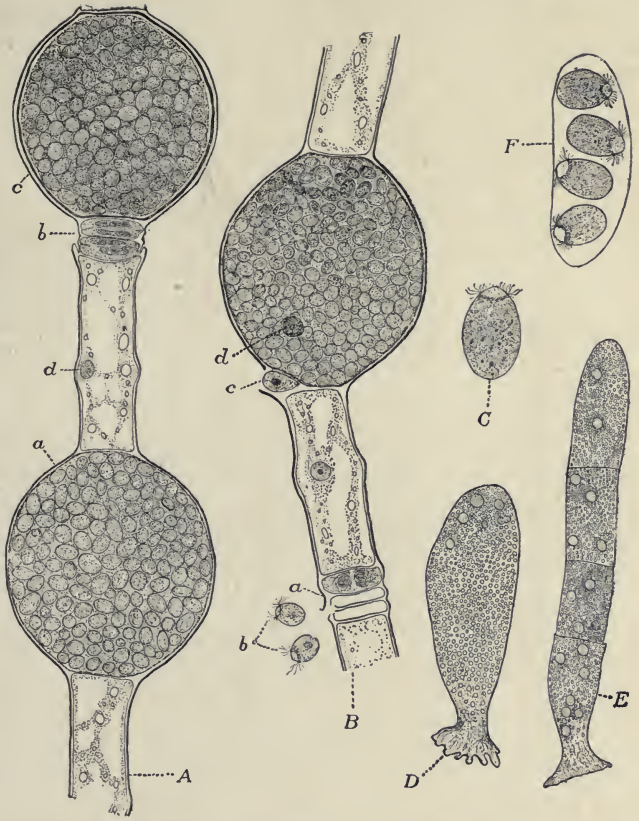


FIG. 7. *Edogonium nodosum*, a Conferva form: *A*, portion of a filament showing a vegetative cell with its nucleus (*d*), an oogonium (*a*) filled by an egg packed with food material, a second oogonium (*c*) containing a fertilized egg or oospore as shown by the heavy wall, and two antheridia (*b*), each containing two sperms; *B*, another filament showing antheridia (*a*) from which two sperms (*b*) have escaped, a vegetative cell with its nucleus, and an oogonium which a sperm (*c*) has entered and is coming in contact with the egg whose nucleus (*d*) may be seen; *C*, a zoospore which has been formed in a vegetative cell, showing the crown of cilia and the clear apex, as in the sperms; *D*, a zoospore producing a new filament, putting out a holdfast at base and elongating; *E*, a further stage of development; *F*, the four zoospores formed by the oospore when it germinates. —CALDWELL, except *C* and *F*, which are after PRINGSHEIM.

(§ 13). The other cells are longer than in *Ulothrix*, each cell containing a single nucleus and apparently several chloroplasts, but really there is but one large complex chloroplast.

The cells of the filament have the power of division, thus increasing the length of the filament. Any cell also may act as a sporangium, the contents of a mother cell organizing a single large asexual spore, which is a zoospore. The zoospore escapes from the mother cell into the water, and at its more pointed clear end there is a little crown of cilia, by means of which it swims about rapidly (Fig. 7, *C*). After moving about for a time the zoospore comes to rest, attaches itself by its clear end to some support, elongates, begins to divide, and develops a new filament (Fig. 7, *D*, *E*).

Other cells of the filament become very different from the ordinary cells, swelling out into globular form (Fig. 7, *A*, *B*), and each such cell organizes within itself a single large egg (oosphere). As the egg is a female gamete, the large globular cell which produces it, and which is differentiated from the other cells of the body, is the oogonium. A perforation in the oogonium wall is formed for the entrance of sperms.

Other cells in the same filament, or in some other filament, are observed to differ from the ordinary cells in being much shorter, as though an ordinary cell had been divided several times without subsequent elongation (Fig. 7, *A*, *f*, *B*, *a*). In each of these short cells one or two sperms are organized, and therefore each short cell is an antheridium. When the sperms are set free they are seen to resemble very small zoospores, having the same little crown of cilia at one end.

The sperms swim actively about in the vicinity of the oogonia, and sooner or later one enters the oogonium through the perforation provided in the wall, and fuses with the egg (Fig. 7, *B*, *c*). As a result of this act of fertilization an oospore is formed, which organizes a firm wall

about itself. This firm wall indicates that the oospore is not to germinate immediately, but is to pass into a resting condition. Spores which form heavy walls and pass into the resting condition are often spoken of as "resting spores," and it is very common for the zygotes and oospores to be resting spores. These resting spores enable the plant to endure through unfavorable conditions, such as failure of food supply, cold, drought, etc. When favorable conditions return, the protected resting spore is ready for germination.

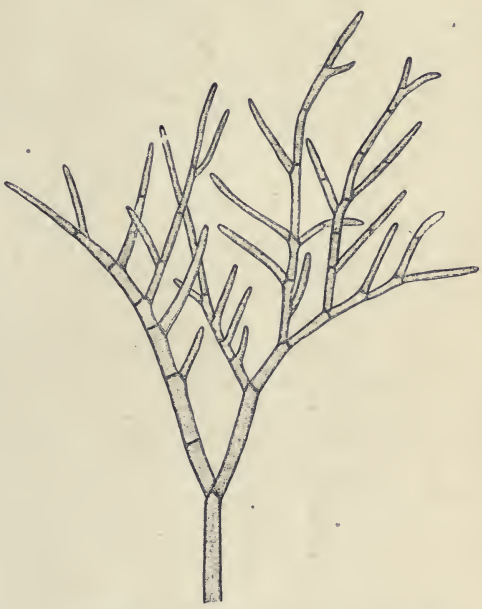


FIG. 8. *Cladophora*, a branching green alga, a very small part of the plant being shown. The branches arise at the upper ends of cells, and the cells are cœnocytic.—CALDWELL.

When the oospore of *Edogonium* germinates it does not develop directly into a new filament, but the contents become organized into four zoospores (Fig. 7, *F*), which escape, and each zoospore develops a filament. In this way each oospore may give rise to four filaments.

It is evident that *Edogonium* is a heterogamous plant, and is another one of the Conferva forms. Conferva bodies are not always simple filaments, as are those of *Ulothrix* and *Edogonium*, but they are sometimes extensively branching filaments, as in *Cladophora*, a green alga very common

in rivers and lakes (Fig. 8). The cells are long and densely crowded with chloroplasts; and in certain cells at the tips of branches large numbers of zoospores are formed, which have two cilia at the pointed end, and hence are said to be *biciliate.*

25. **Vaucheria.**—This is one of the most common of the Green Algæ, found in felt-like masses of coarse filaments in shallow water and on muddy banks, and often called "green

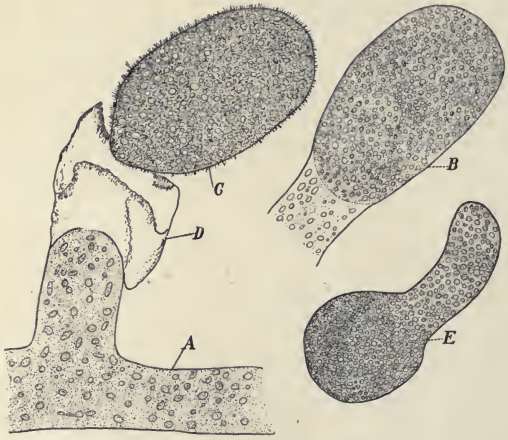


FIG. 9. *Vaucheria geminata*, a Siphon form, showing a portion of the cœnocytic body (*A*) which has sent out a branch at the tip of which a sporangium (*B*) formed, within which a large zoospore was organized, and from which (*D*) it is discharged later as a large multiciliate body (*C*), which then begins the development of a new cœnocytic body (*E*).—CALDWELL.

felt." The filament is very long, and usually branches extensively, but its great peculiarity is that there is no partition wall in the whole body, which forms one long continuous cavity (Figs. 9, 11). This is sometimes spoken of as a one-celled body, but it is a mistake. Imbedded in the extensive cytoplasm mass, which fills the whole cavity, there are not only very numerous chloroplasts, but also numerous nuclei. As has been said, a single nucleus with some cyto-

plasm organized about it is a cell, whether it has a wall or not. Therefore the body of *Vaucheria* is made up of as many cells as there are nuclei, cells whose protoplasmic structures have not been kept separate by cell walls. Such a body, made up of numerous cells, but with no partitions, is called a *cœnocyte*, or it is said to be *cœnocytic*. *Vaucheria* represents a great group of Chlorophyceæ whose members have cœnocytic bodies, and on this account they are called the Siphon forms.

Vaucheria produces very large zoospores. The tip of a branch becomes separated from the rest of the body by a partition and thus acts as a sporangium (Fig. 9, *B*). In this improvised sporangium the whole of the contents organize a single large zoospore, which is ciliated all over, escapes by squeezing through a perforation in the wall (Fig. 9, *C*), swims about for a time, and finally develops another *Vaucheria* body (Figs. 9, *E*, 10). It should be said that this large body, called a zoospore and acting like one, is really a mass of small biciliate zoospores, just as the

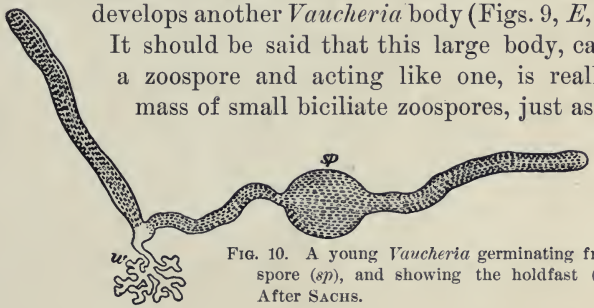


Fig. 10. A young *Vaucheria* germinating from a spore (*sp*), and showing the holdfast (*w*).—After Sachs.

apparently one-celled vegetative body is really composed of many cells. In this large compound zoospore there are many nuclei, and in connection with each nucleus two cilia are developed. Each nucleus with its cytoplasm and two cilia represents a small biciliate zoospore, such as those of *Cladophora*, § 24.

Antheridia and oogonia are also developed. In a common form these two sex organs appear as short special branches developed on the side of the large cœnocytic body,

and cut off from the general cavity by partition walls (Fig. 11). The oogonium becomes a globular cell, which usually

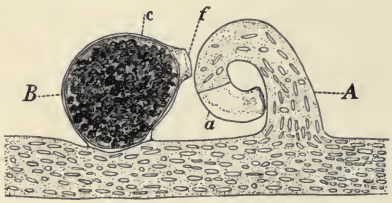


FIG. 11. *Vaucheria sessilis*, a Siphon form, showing a portion of the cœnocytic body, an antheridial branch (*A*) with an empty antheridium (*a*) at its tip, and an oogonium (*B*) containing an oospore (*c*) and showing the opening (*f*) through which the sperms passed to reach the egg.—CALDWELL.

develops a perforated break for the entrance of the sperms, and organizes within itself a single large egg (Fig. 11, *B*). The antheridium is a much smaller cell, within which numerous very small sperms are formed (Fig. 11, *A*, *a*). The sperms are discharged, swarm about the oogonium, and finally one passes through the break and fuses with the egg, the result being an oospore. The oospore organizes a thick wall and becomes a resting spore.

FIG. 12. *Botrydium*, one of the Siphon forms of green algæ, the whole body containing one continuous cavity, with a bulbous, chlorophyll-containing portion, and root-like branches which penetrate the mud in which the plant grows.—CALDWELL.

It is evident that *Vaucheria* is heterogamous, but all the other Siphon forms are isogamous, of which *Botrydium* may be taken as an illustration (Fig. 12).

26. **Spirogyra.**—This is one of the commonest of the "pond scums," occurring in slippery and often frothy masses of delicate filaments floating in still water or about

springs. The filaments are simple, and are not anchored by a special basal cell, as in *Ulothrix* and *Edogonium*. The

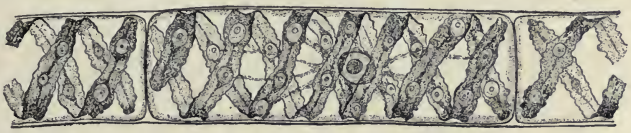


FIG. 13. *Spirogyra*, a Conjugate form, showing one complete cell and portions of two others. The band-like chloroplasts extend in a spiral from one end of the cell to the other, in them are imbedded nodule-like bodies (*pyrenoids*), and near the center of the cell the nucleus is swung by radiating strands of cytoplasm.—CALDWELL.

cells contain remarkable chloroplasts, which are bands passing spirally about within the cell wall. These bands may

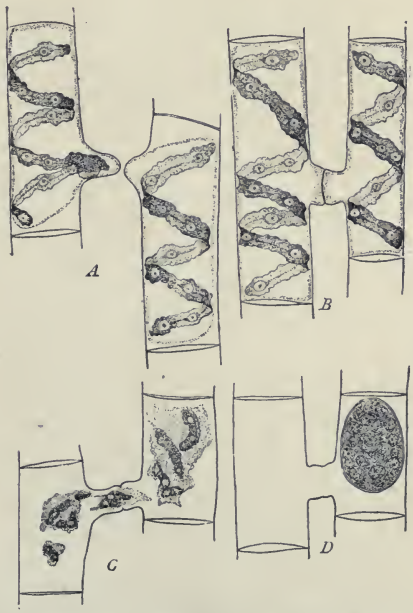


FIG. 14. *Spirogyra*, showing conjugation: *A*, conjugating tubes approaching each other; *B*, tubes in contact but end walls not absorbed; *C*, tube complete and contents of one cell passing through; *D*, a completed zygospore.—CALDWELL.

be solitary or several in a cell, and form very striking and conspicuous objects (Figs. 13, 14).

Spirogyra and its associates are further peculiar in producing no asexual spores, and also in the method of sexual reproduction. Two adjacent filaments put out tubular processes toward one another. A cell of one filament sends out a process which seeks to meet a corresponding process from a cell of the other filament. When the tips of two such processes come together, the end walls disappear,

FIG. 15. *Spirogyra*, showing some common exceptions. At *A* two cells have been connected by a tube, but without fusion a zygote has been organized in each cell; also, the upper cell to the left has attempted to conjugate with the cell to the right. At *B* there are cells from three filaments, the cells of the central one having conjugated with both of the others.—CALDWELL.

and a continuous tube extending between the two cells is organized (Figs. 14, 15). When many of the cells of two parallel filaments become thus united, the appearance is that of a ladder, with the filaments as the side pieces, and the connecting tubes as the rounds.

While the connecting tube is being developed the contents of the two cells are organizing, and after the completion of the tube the contents of one cell pass through and enter the other cell, fuse with its contents, and a sexual

spore is organized. As the gametes look alike, the process is conjugation, and the sex spore is a zygote, which, with its heavy wall, is recognized to be a resting spore. At the beginning of each growing season, the well-protected zygotes which have endured the winter germinate directly into new *Spirogyra* filaments.

On account of this peculiar style of sexual reproduction, in which gametes are not discharged, but reach each other through special tubes, *Spirogyra* and its allies are called Conjugate forms—that is, forms whose bodies are "yoked together" during the fusion of the gametes.

In some of the Conjugate forms the zygote is formed in the connecting tube (Fig. 16, *A*), and sometimes zygotes are formed without conjugation (Fig. 16, *B*). Among the Conjugate forms the Desmids are of great interest and beauty, being one-celled, the cells being organized into two distinct halves (Fig. 17).

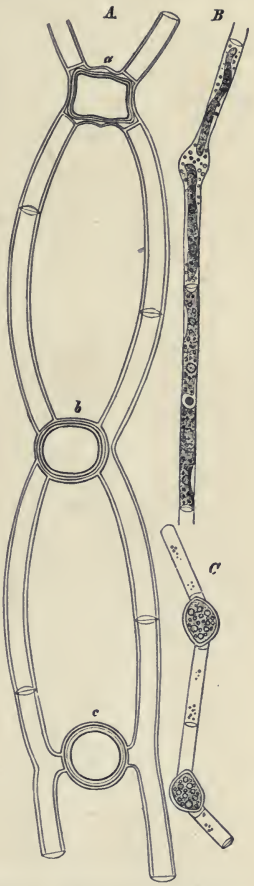


FIG. 16. Two Conjugate forms: *A* (*Mougeotia*), showing formation of zygote in conjugating tube; *B*, *C* (*Gonatonema*), showing formation of zygote without conjugation. —After WITTROCK.

27. **Conclusions.** — The Green Algæ, as indicated by the illustrations given above, include simple one-celled forms which reproduce by fission, but they are chiefly filamentous forms, simple or branching. These filamentous bodies either have the cells separated from one another

by walls, or they are cœnocytic, as in the Siphon forms. The characteristic asexual spores are zoospores, but these may be wanting, as in the Conjugate forms. In addition to asexual reproduction, both isogamy and heterogamy are developed, and both zygotes and oospores are resting spores.

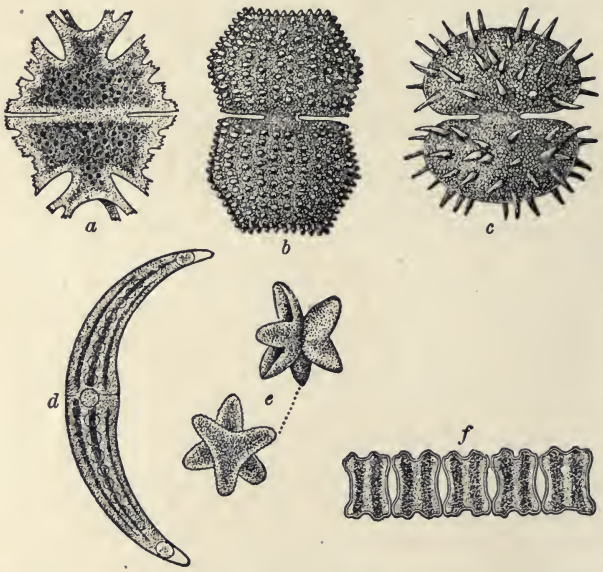


FIG. 17. A group of Desmids, one-celled Conjugate forms, showing various patterns, and the cells organized into distinct halves.—After KERNER.

The Green Algæ are of special interest in connection with the evolution of higher plants, which are supposed to have been derived from them.

3. PHÆOPHYCEÆ (*Brown Algæ*)

28. **General characters.**—The Blue-green Algæ and the Green Algæ are characteristic of fresh water, but the Brown Algæ, or "kelps," are almost all marine, being very charac-

teristic coast forms. All of them are anchored by holdfasts, which are sometimes highly developed root-like structures; and the yellow, brown, or olive-green floating bodies are buoyed in the water usually by the aid of floats or air-bladders, which are often very conspicuous. The kelps are most highly developed in the colder waters, and form much of the "wrack," "tangle," etc., of the coasts. The group is well adapted to live exposed to waves and currents with its strong holdfasts, air-bladders, and tough leathery bodies. It is what is known as a *specialized group*—that is, one which has become highly organized for certain special conditions. It is not our purpose to consider such a specialized group in any detail, as it does not usually help to explain the structures of higher groups.

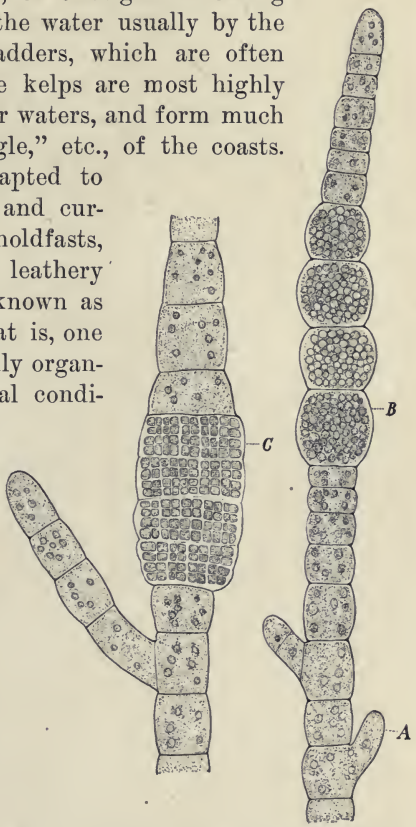


FIG. 18. A brown alga (*Ectocarpus*), showing a body consisting of a simple filament which puts out branches (*A*), some sporangia (*B*) containing zoospores, and gametangia (*C*) containing gametes.—CALDWELL.

29. **The plant body.**—There is very great diversity in the structure of the plant body. Some of them, as *Ectocarpus* (Fig. 18), are filamentous forms, like the Confervas among the Green Algæ, but others are very much more complex. The thallus of *Laminaria* is like a huge floating leaf, frequently nine to ten

FIG. 18*a*. A group of brown seaweeds (*Laminarias*). Note the various habits of the plant body with its leaf-like thallus and root-like holdfasts.—After KERNER.

feet long, whose stalk develops root-like holdfasts (Fig. 18*a*). The largest body is developed by an Antarctic *Laminaria* form, which rises to the surface from a sloping bottom with a floating thallus six hundred to nine hundred feet long. Other forms rise from the sea bottom like trees, with thick trunks, numerous branches, and leaf-like appendages.

The common *Fucus*, or "rock weed," is ribbon-form and constantly branches by forking at the tip (Fig. 19). This method of branching is called *dichotomous*, as distinct from that in which branches are put out from the sides of the axis (*monopodial*). The swollen air-bladders distributed throughout the body are very conspicuous.

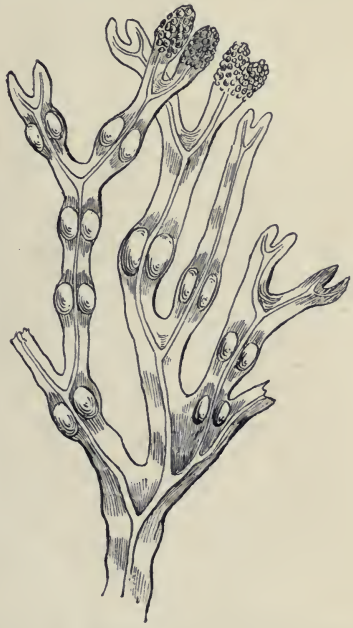


Fig. 19. Fragment of a common brown alga (*Fucus*), showing the body with dichotomous branching and bladder-like air-bladders.—After Luerssen.

The most differentiated thallus is that of *Sargassum* (Fig. 20), or "gulf weed," in which there are slender branching stem-like axes bearing lateral members of various kinds, some of them like ordinary foliage leaves; others are floats or air-bladders, which sometimes resemble clusters of berries; and other branches bear the sex organs. All of these structures are but different regions of a branching thallus. *Sargassum* forms are often torn from their anchorage by the waves and carried away from the coast by currents, collecting in the great sea eddies

produced by oceanic currents and forming the so-called "Sargasso seas," as that of the North Atlantic.

FIG. 20. A portion of a brown alga (*Sargassum*), showing the thallus differentiated into stem-like and leaf-like portions, and also the bladder-like floats.—After BENNETT and MURRAY.

30. **Reproduction.**—The two main groups of Brown Algæ differ from each other in their reproduction. One, represented by the Laminarias and a majority of the forms, produces zoospores and is isogamous (Fig. 18). The zoospores and gametes are peculiar in having the two cilia attached at one side rather than at an end; and they resemble each other very closely, except that the gametes fuse in pairs and form zygotes.

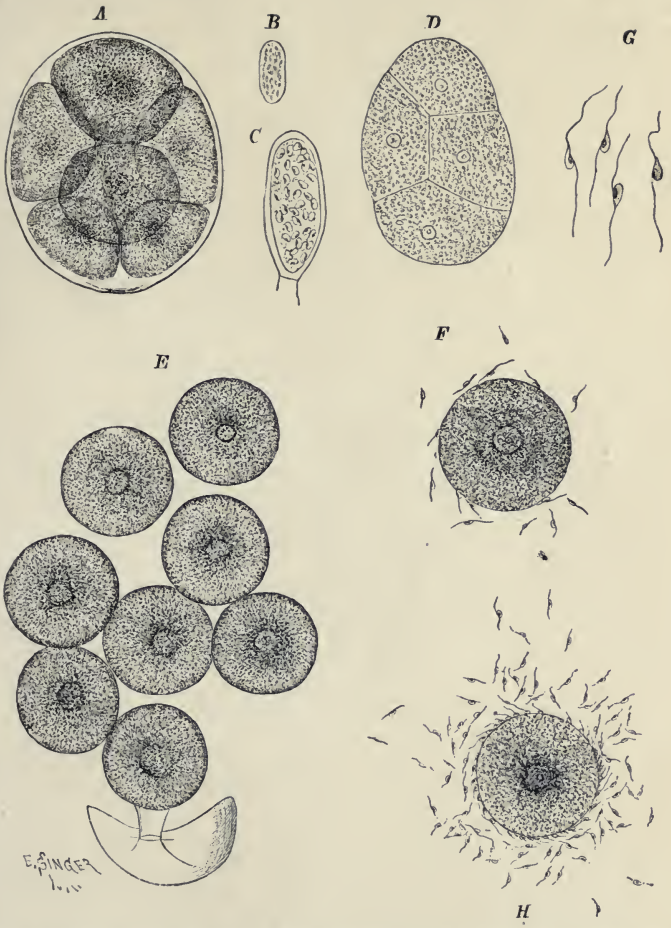


FIG. 21. Sexual reproduction of *Fucus*, showing the eight eggs (six in sight) discharged from the oogonium and surrounded by a membrane (*A*), eggs liberated from the membrane (*E*), antheridium containing sperms (*C*), the discharged laterally biciliate sperms (*G*), and eggs surrounded by swarming sperms (*F*, *H*).—After SINGER.

The other group, represented by *Fucus* (Fig. 21), produces no asexual spores, but is heterogamous. A single oogonium usually forms eight eggs (Fig. 21, *A*), which are discharged and float freely in the water (Fig. 21, *E*). The antheridia (Fig. 21, *C*) produce numerous minute laterally biciliate sperms, which are discharged (Fig. 21, *G*), swim in great numbers about the large eggs (Fig. 21, *F*, *H*), and finally one fuses with an egg, and an oospore is formed. As the sperms swarm very actively about the egg and impinge against it they often set it rotating. Both antheridia and oogonia are formed in cavities of the thallus.

4. Rhodophyceæ (*Red Algæ*)

31. **General characters.**—On account of their red coloration these forms are often called *Florideæ*. They are mostly marine forms, and are anchored by holdfasts of various kinds. They belong to the deepest waters in which Algæ grow, and it is probable that the red coloring matter which characterizes them is associated with the depth at which they live. The Red Algæ are also a highly specialized line, and will be mentioned very briefly.

Fig. 22. A red alga (*Gigartina*), showing branching habit, and "fruit bodies."—After Schenck.

32. **The plant body.**—The Red Algæ, in general, are more delicate than the Brown Algæ, or kelps, their graceful forms, delicate texture, and brightly tinted bodies (shades of red, violet, dark purple,

FIG. 23. A red alga (*Callophyllis*), with a greatly branched body composed of thin plates of cells.—CALDWELL.

FIG. 24. A red alga (*Dasya*), showing a finely divided thallus body.—CALDWELL.

Fig. 25. A red alga (*Rabdonia*), showing holdfasts and branching thallus body.—Caldwell.

FIG. 26. A red alga (*Ptilota*), whose branching body resembles moss.—CALDWELL.

and reddish-brown) making them very attractive. They show the greatest variety of forms, branching filaments, ribbons, and filmy plates prevailing, sometimes branching very profusely and delicately, and resembling mosses of fine texture (Figs. 22, 23, 24, 25, 26). The differentiation of the thallus into root and stem and leaf-like structures is also common, as in the Brown Algæ.

33. **Reproduction.**—Red Algæ are very peculiar in both their asexual and sexual reproduction. A sporangium produces just four asexual spores, but they have no cilia and no power of motion. They can not be called zoospores, therefore, and as each sporangium always produces just four, they have been called *tetraspores* (Fig. 27).

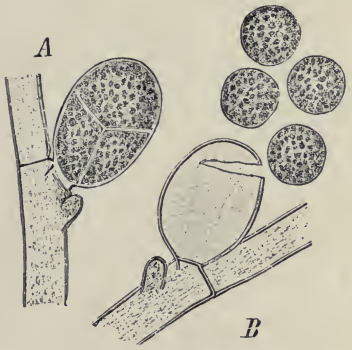


FIG. 27. A red alga (*Callithamnion*), showing sporangium (*A*), and the tetraspores discharged (*B*).—After THURET.

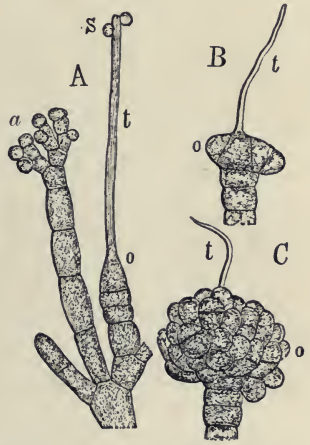


FIG. 28. A red alga (*Nemalion*); *A*, sexual branches, showing antheridia (*a*), oogonium (*o*) with its trichogyne (*t*), to which are attached two spermatia (*s*); *B*, beginning of a cystocarp (*o*), the trichogyne (*t*) still showing; *C*, an almost mature cystocarp (*o*), with the disorganizing trichogyne (*t*).—After VINES.

Red Algæ are also heterogamous, but the sexual process has been so much and so variously modified that it is very poorly understood. The antheridia (Fig. 28, *A*, *a*) develop sperms which, like the tetraspores, have no cilia and no power of motion. To dis-

tinguish them from the ciliated sperms, or spermatozoids, which have the power of locomotion, these motionless male gametes of the Red Algæ are usually called *spermatia* (singular, *spermatium*) (Fig. 28, *A*, *s*).

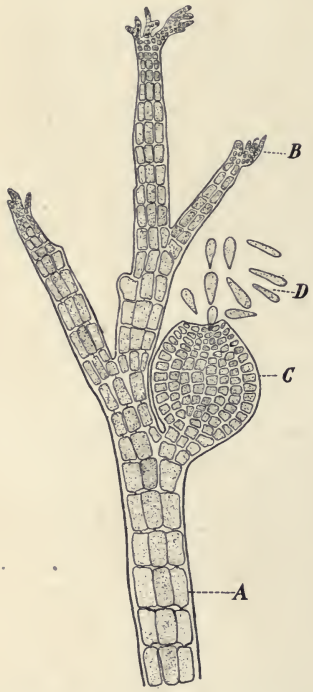


Fig. 29. A branch of *Polysiphonia*, one of the red algæ, showing the rows of cells composing the body (*A*), small branches or hairs (*B*), and a cystocarp (*C*) with escaping spores (*D*) which have no cilia (carpospores).—Caldwell.

The oogonium is very peculiar, being differentiated into two regions, a bulbous base and a hair-like process (*trichogyne*), the whole structure resembling a flask with a long, narrow neck, excepting that it is closed (Fig. 28, *A*, *o*, *t*). Within the bulbous part the egg, or its equivalent, is organized; a spermatium attaches itself to the trichogyne (Fig. 28, *A*, *s*); at the point of contact the two walls become perforated, and the contents of the spermatium thus enter the trichogyne, and so reach the bulbous base of the oogonium. The above account represents the very simplest conditions of the process of fertilization in this group, and gives no idea of the great and puzzling complexity exhibited by the majority of forms.

After fertilization the trichogyne wilts, and the bulbous base in one way or another develops a conspicuous structure called the *cystocarp* (Figs. 28, 29), which is a case containing asexual spores; in other words, a spore case, or kind of sporangium. In the life history of a red alga, there-

fore, two sorts of asexual spores are produced: (1) the *tetraspores*, developed in ordinary sporangia; and (2) the *carpospores*, developed in the cystocarp, which has been produced as the result of fertilization.

OTHER CHLOROPHYLL-CONTAINING THALLOPHYTES

34. **Diatoms.**—These are peculiar one-celled forms, which occur in very great abundance in fresh and salt waters.

FIG. 30. A group of Diatoms: *c* and *d*, top and side views of the same form; *e*, colony of stalked forms attached to an alga; *f* and *g*, top and side views of the form shown at *e*; *h*, a colony; *i*, a colony, the top and side view shown at *k*.—After KERNER.

They are either free-swimming or attached by gelatinous stalks; solitary, or connected in bands or chains, or imbedded in gelatinous tubes or masses. In form they are rod-shaped, boat-shaped, elliptical, wedge-shaped, straight or curved (Fig. 30).

The chief peculiarity is that the wall is composed of two valves, one of which fits into the other like the two parts of a pill box. This wall is so impregnated with silica that it is practically indestructible, and siliceous skeletons of diatoms are preserved abundantly in certain rock deposits. They multiply by cell division in a peculiar way, and some of them have been observed to conjugate.

Fig. 31. A common *Chara*, showing tip of main axis. —After Strasburger.

They occur in such numbers in the ocean that they form a large part of the free-swimming forms on the surface of the sea, and doubtless showers of the siliceous skeletons are constantly falling on the sea bottom. There are certain deposits known as "siliceous earths," which are simply masses of fossil diatoms.

Diatoms have been variously placed in schemes of classification. Some have put them among the Brown Algæ because they contain a brown coloring matter; others have placed them in the Conjugate forms among the Green Algæ on account of the occasional conjugation that has been observed. They are so different from other forms, however, that it seems best to keep them separate from all other Algæ.

35. **Characeæ.**—These are commonly called "stoneworts," and are often included as a group of Green Algæ, as they seem to be Thallophytes, and have no other coloring matter than chlorophyll. However, they are so peculiar that they are better kept by themselves among the Algæ. They are such

specialized forms, and are so much more highly organized than all other Algæ, that they will be passed over here with a bare mention. They grow in fresh or brackish waters, fixed to the bottom, and forming great masses. The cylindrical stems are jointed, the joints sending out circles of branches, which repeat the jointed and branching habit (Fig. 31).

The walls become incrusted with a deposit of lime, which makes the plants harsh and brittle, and has suggested the name "stoneworts." In addition to the highly organized nutritive body, the antheridia and oogonia are peculiarly complex, being entirely unlike the simple sex organs of the other Algæ.

CHAPTER V

THALLOPHYTES: FUNGI

36. **General characters.**—In general, Fungi include Thallophytes which do not contain chlorophyll. From this fact it follows that they can not manufacture food entirely out of inorganic material, but are dependent for it upon other plants or animals. This food is obtained in two general ways, either (1) directly from the living bodies of plants or animals, or (2) from dead bodies or the products of living bodies. In the first case, in which living bodies are attacked, the attacking fungus is called a *parasite*, and the plant or animal attacked is called the *host*. In the second case, in which living bodies are not attacked, the fungus is called a *saprophyte*. Some Fungi can live only as parasites, or as saprophytes, but some can live in either way.

Fungi form a very large assemblage of plants, much more numerous than the Algæ. As many of the parasites attack and injure useful plants and animals, producing many of the so-called "diseases," they are forms of great interest. Governments and Experiment Stations have expended a great deal of money in studying the injurious parasitic Fungi, and in trying to discover some method of destroying them or of preventing their attacks. Many of the parasitic forms, however, are harmless; while many of the saprophytic forms are decidedly beneficial.

It is generally supposed that the Fungi are derived from the Algæ, having lost their chlorophyll and power of independent living. Some of them resemble certain Algæ so closely that the connection seems very plain; but others

have been so modified by their parasitic and saprophytic habits that they have lost all likeness to the Algæ, and their connection with them is very obscure.

37. **The plant body.**—Discarding certain problematical forms, to be mentioned later, the bodies of all true Fungi are organized upon a uniform general plan, to which they can all be referred (Fig. 32). A set of colorless branching

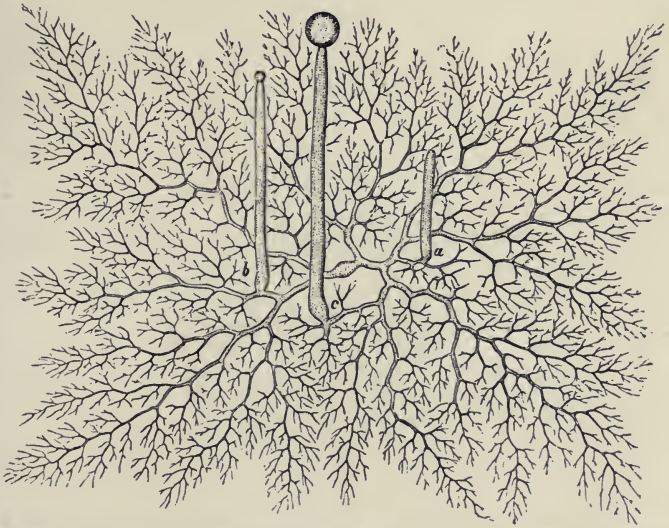


FIG. 32. A diagrammatic representation of *Mucor*, showing the profusely branching mycelium, and three vertical hyphæ (sporophores), sporangia forming on *b* and *c*. —After ZOPF.

filaments, either isolated or interwoven, forms the main working body, and is called the *mycelium*. The interweaving may be very loose, the mycelium looking like a delicate cobweb; or it may be close and compact, forming a felt-like mass, as may often be seen in connection with preserved fruits. The individual threads are called *hyphæ* (singular, *hypha*) or *hyphal threads*. The mycelium is in contact with its source of food supply, which is called the *substratum*.

From the hyphal threads composing the mycelium vertical ascending branches arise, which are set apart to produce the asexual spores, which are scattered and produce new mycelia. These branches are called *ascending hyphæ* or *sporophores*, meaning "spore bearers."

Sometimes, especially in the case of parasites, special descending branches are formed, which penetrate the substratum or host and absorb the food material. These special absorbing branches are called *haustoria*, meaning "absorbers."

Such a mycelial body, with its sporophores, and perhaps haustoria, lies either upon or within a dead substratum in the case of saprophytes, or upon or within a living plant or animal in the case of parasites.

38. **The subdivisions.**—The classification of Fungi is in confusion on account of lack of knowledge. They are so much modified by their peculiar life habits that they have lost or disguised the structures which prove most helpful in classification among the Algæ. Four groups will be presented, often made to include all the Fungi, but doubtless they are insufficient and more or less unnatural.

The constant termination of the group names is *mycetes*, a Greek word meaning "fungi." The prefix in each case is intended to indicate some important character of the group. The names of the four groups to be presented are as follows: (1) *Phycomycetes* ("Alga-Fungi"), referring to the fact that the forms plainly resemble the Algæ; (2) *Ascomycetes* ("Ascus-Fungi"); (3) *Æcidiomycetes* ("Æcidium-Fungi"); (4) *Basidiomycetes* ("Basidium-Fungi"). Just what the prefixes *ascus*, *æcidium*, and *basidium* mean will be explained in connection with the groups. The last three groups are often associated together under the name *Mycomycetes*, meaning "Fungus-Fungi," to distinguish them from the Phycomycetes, or "Alga-Fungi," referring to the fact that they do not resemble the Algæ, and are only like themselves.

One of the ordinary life processes which seems to be seriously interfered with by the saprophytic and parasitic habit is the sexual process. At least, while sex organs and sexual spores are about as evident in Phycomycetes as in Algæ, they are either obscure or wanting in the Mycomycete groups.

1. Phycomycetes (*Alga-Fungi*)

39. **Saprolegnia.**—This is a group of "water-moulds," with aquatic habit like the Algæ. They live upon the dead bodies of water plants and animals (Fig. 33), and sometimes attack living fish, one kind being very destructive to young fish in hatcheries. The hyphæ composing the mycelium are cœnocytes, as in the Siphon forms.

Sporangia are organized at the ends of branches by forming a partition wall separating the cavity of the tip from the general cavity (Fig. 33, *B*). The tip becomes more or less swollen, and within it are formed numerous biciliate zoospores, which are discharged into the water (Fig. 33, *C*), swim about for a short time, and rapidly form new mycelia. The process is very suggestive of *Cladophora* and *Vaucheria*. Oogonia and antheridia are also formed at the ends of the branches (Fig. 33, *F*), much as in *Vaucheria*. The oogonia are spherical, and form one and sometimes many eggs (Fig. 33, *D*, *E*). The antheridia are formed on branches near the oogonia. An antheridium comes in contact with an oogonium, and sends out a delicate tube which pierces the oogonium wall (Fig. 33, *F*). Through this tube the contents of the antheridium pass, fuse with the egg, and a heavy-walled oospore or resting spore is the result.

It is an interesting fact that sometimes the contents of an antheridium do not enter an oogonium, or antheridia may not even be formed, and still the egg, without fertilization, forms an oospore which can germinate. This peculiar

habit is called *parthenogenesis*, which means reproduction by an egg without fertilization.

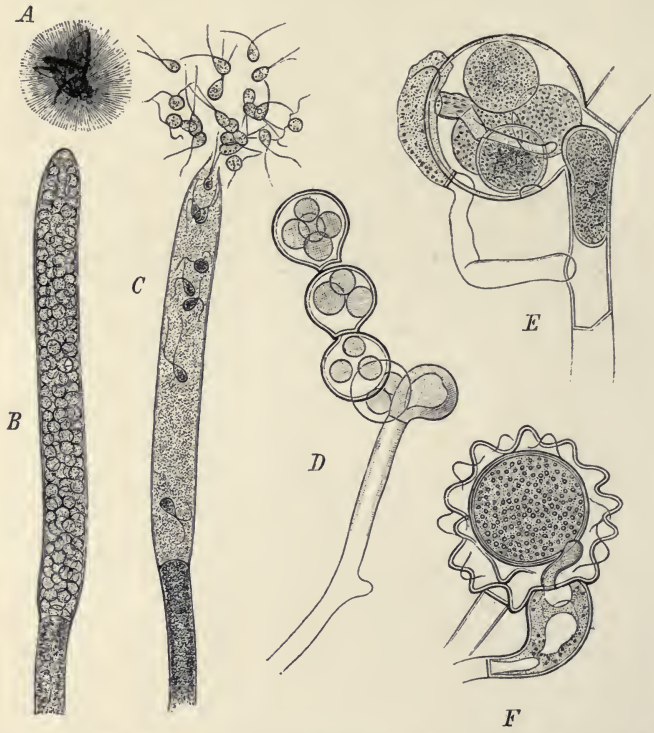


FIG. 33. A common water mould (*Saprolegnia*): *A*, a fly from which mycelial filaments of the parasite are growing; *B*, tip of a branch organized as a sporangium; *C*, sporangium discharging biciliate zoospores; *F*, oogonium with antheridium in contact, the tube having penetrated to the egg; *D* and *E*, oogonia with several eggs.—*A*-*C* after THURET, *D*-*F* after DEBARY.

40. **Mucor.**—One of the most common of the Mucors, or "black moulds," forms white furry growths on damp bread, preserved fruits, manure heaps, etc. It is therefore a saprophyte, the cœnocytic mycelium branching extensively through the substratum (Fig. 34).

Erect sporophores arise from it in abundance, and at the top of each sporophore a globular sporangium is formed, within which are numerous small asexual spores (Figs. 35,

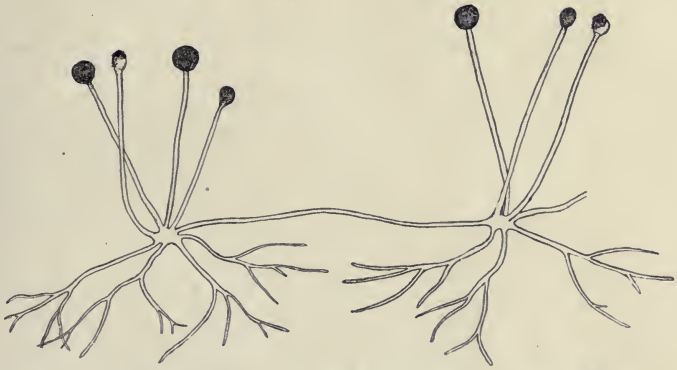


Fig. 34. Diagram showing mycelium and sporophores of a common *Mucor*.—Caldwell.

36). The sporangium wall bursts (Fig. 37), the light spores are scattered by the wind, and, falling upon a suitable substratum, germinate and form new mycelia. It is evident that these asexual spores are not zoospores, for there is no water medium and swimming is impossible. This method of transfer being impossible, the spores are scattered by currents of air, and must be correspondingly light and powdery. They are usually spoken of simply as "spores," without any prefix.

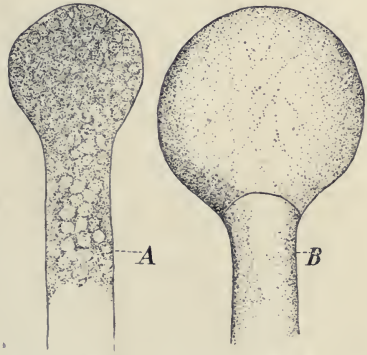


Fig. 35. Forming sporangia of *Mucor*, showing the swollen tip of the sporophore (*A*), and a later stage (*B*), in which a wall is formed separating the sporangium from the rest of the body.—Caldwell.

While the ordinary method of reproduction through the growing season is by means of these rapidly germinating spores, in certain conditions a sexual process is observed, by which a heavy-walled sexual spore is formed as a resting spore, able to outlive unfavorable conditions. Branches arise from the hyphæ of the mycelium just as in the forma-

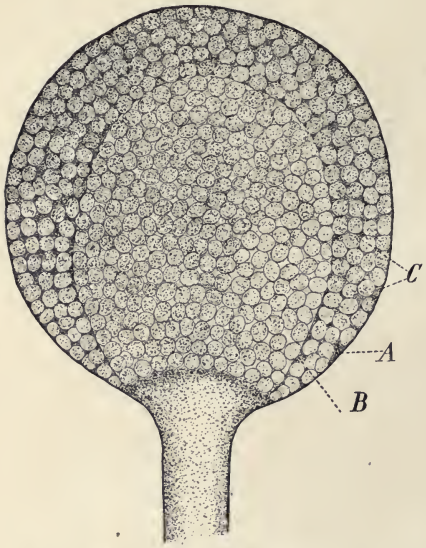


FIG. 36. Mature sporangium of *Mucor*, showing the wall (*A*), the numerous spores (*C*), and the columella (*B*)—that is, the partition wall pushed up into the cavity of the sporangium. —CALDWELL.

FIG. 37. Bursted sporangium of *Mucor*, the ruptured wall not being shown, and the loose spores adhering to the columella.—CALDWELL.

tion of sporophores (Fig. 38). Two contiguous branches come in contact by their tips (Fig. 38, *A*), the tips are cut off from the main cœnocytic body by partition walls (Fig. 38, *B*), the walls in contact disorganize, the contents of the two tip cells fuse, and a heavy-walled sexual spore is the result (Fig. 38, *C*). It is evident that the process is conjugation, suggesting the Conjugate forms among the

Algæ; that the sexual spore is a zygote; and that the two pairing tip cells cut off from the main body by partition walls are gametangia. *Mucor*, therefore, is isogamous.

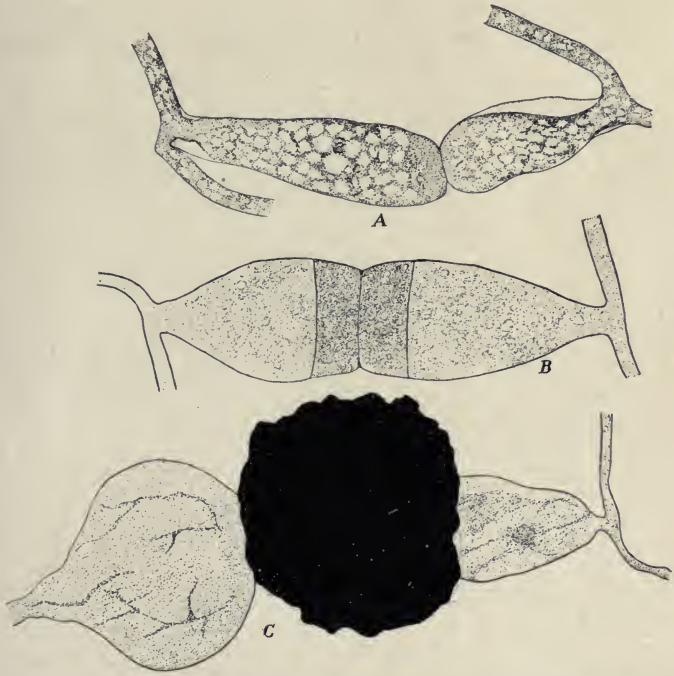


FIG. 38. Sexual reproduction of *Mucor*, showing tips of sex branches meeting (*A*), the two gametangia cut off by partition walls (*B*), and the heavy-walled zygote (*C*).—CALDWELL.

41. **Peronospora.**—These are the "downy mildews," very common parasites on seed plants as hosts, one of the most common kind attacking grape leaves. The mycelium is cœnocytic and entirely internal, ramifying among the tissues within the leaf, and piercing the living cells with haustoria which rapidly absorb their contents (Fig. 39). The presence of the parasite is made known by discolored and

finally deadened spots on the leaves, where the tissues have been killed.

From this internal mycelium numerous sporophores arise, coming to the surface of the host and securing the scattering of their spores, which fall upon other leaves and germinate, the new mycelia penetrating among the tissues and beginning their ravages. The sporophores, after rising above the surface of the leaf, branch freely; and many of them rising near together, they form little velvety patches on the surface, suggesting the name "downy mildew."

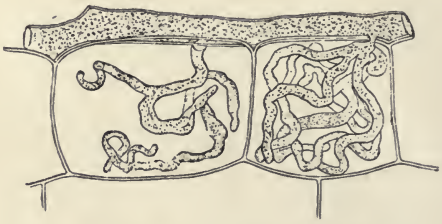


FIG. 39. A branch of *Peronospora* in contact with two cells of a host plant, and sending into them its large haustoria.—After DEBARY.

FIG. 40. *Peronospora*, one of the Phycomycetes, showing at *a* an oogonium (*o*) containing an egg, and an antheridium (*n*) in contact; at *b* the antheridial tube penetrating the oogonium and discharging the contents of the antheridium into the egg; at *c* the oogonium containing the oospore or resting spore.—After DEBARY.

In certain conditions special branches arise from the mycelium, which organize antheridia and oogonia, and remain within the host (Fig. 40). The oogonium is of the usual spherical form, organizing a single egg. The an-

theridium comes in contact with the oogonium, puts out a tube which pierces the oogonium wall and enters the egg, into which the contents of the antheridium are discharged, and fertilization is effected. The result is a heavy-walled oospore. As the oospores are not for immediate germination, they are not brought to the surface of the host and scattered, as are the asexual spores. When they are ready to germinate, the leaves bearing them have perished and the oospores are liberated.

42. **Conclusions.**—The cœnocytic bodies of the whole group are very suggestive of the Siphon forms among Green Algæ, as is also the method of forming oogonia and antheridia.

The water-moulds, *Saprolegnia* and its allies, have retained the aquatic habit of the Algæ, and their asexual spores are zoospores. Such forms as *Mucor* and *Peronospora*, however, have adapted themselves to terrestrial conditions, zoospores are abandoned, and light spores are developed which can be carried about by currents of air.

In most of them motile gametes are abandoned. Even in the heterogamous forms sperms are not organized within the antheridium, but the contents of the antheridium are discharged through a tube developed by the wall and penetrating the oogonium. It should be said, however, that a few forms in this group develop sperms, which make them all the more alga-like.

They are both isogamous and heterogamous, both zygotes and oospores being resting spores. Taking the characters all together, it seems reasonably clear that the Phycomycetes are an assemblage of forms derived from Green Algæ (Chlorophyceæ) of various kinds.

2. Ascomycetes (*Ascus- or Sac-Fungi*)

43. **Mildews.**—These are very common parasites, growing especially upon leaves of seed plants, the mycelium spreading over the surface like a cobweb. A very common mil-

dew, *Microsphæra*, grows on lilac leaves, which nearly always show the whitish covering after maturity (Fig. 41). The branching hyphæ show numerous partition walls, and are not cœnocytic as in the Phycomycetes. Small disk-like haustoria penetrate into the superficial cells of the host, anchoring the mycelium and absorbing the cell contents.

Sporophores arise, which form asexual spores in a peculiar way. The end of the sporophore rounds off, almost separating itself from the part below, and becomes a spore or spore-like body. Below this another organizes in the same way, then another, until a chain of spores is developed, easily broken apart and scattered by the wind. Falling upon other suitable leaves, they germinate and form new mycelia, enabling the fungus to spread rapidly. This method of cutting a branch into sections to form spores is called *abstriction*, and the spores formed in this way are called *conidia*, or *conidiospores* (Fig. 43, *B*).

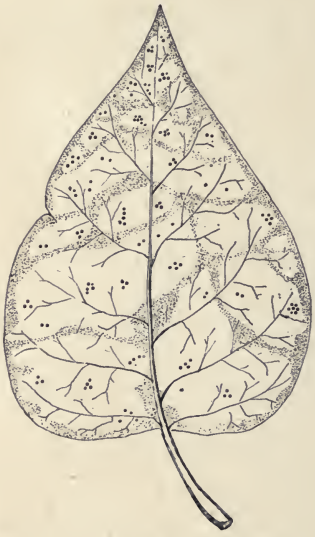


Fig. 41. Lilac leaf covered with mildew (*Microsphæra*), the shaded regions representing the mycelium, and the black dots the ascocarps.—Caldwell.

At certain times the mycelium develops special branches which develop sex organs, but they are seldom seen and may not always occur. An oogonium and an antheridium, of the usual forms, but probably without organizing gametes, come into contact, and as a result an elaborate structure is developed—the *ascocarp*, sometimes called the "spore fruit." These ascocarps appear on the lilac leaves as minute dark dots, each one being

a little sphere, which suggested the name *Microsphæra* (Fig. 41). The heavy wall of the ascocarp bears beautiful branching hair-like appendages (Fig. 42).

Bursting the wall of this spore fruit several very delicate, bladder-like sacs are extruded, and through the transparent wall of each sac there may be seen several spores (Fig. 42). The ascocarp, therefore, is a spore case, just as is the cystocarp of the Red Algæ (§ 33). The delicate sacs within are the *asci*, a word meaning "sacs," and each ascus is evidently a mother cell within which asexual spores are formed. These spores are distinguished from other asexual spores by the name *ascospore*.

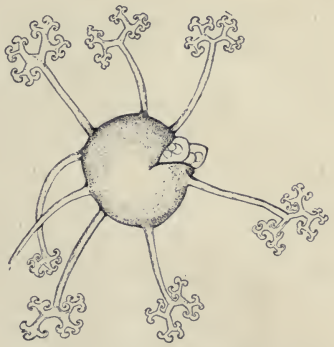


Fig. 42. Ascocarp of the lilac mildew, showing branching appendages and two asci protruding from the ruptured wall and containing ascospores. —Caldwell.

It is these peculiar mother cells, or asci, which give name to the group, and an Ascomycete, Ascus-fungus, or Sac-fungus, is one which produces spores in asci; and an ascocarp is a spore case which contains asci.

In the mildews, therefore, there are two kinds of asexual spores: (1) *conidia*, formed from a hyphal branch by abstriction, by which the mycelium may spread rapidly; and (2) *ascospores*, formed in a mother cell and protected by a heavy case, so that they may bridge over unfavorable conditions, and may germinate when liberated and form new mycelia. The resting stage is not a zygote or an oospore, as in the Algæ and Phycomycetes, no sexual spore probably being formed, but a heavy-walled ascocarp.

44. **Other forms.**—The mildews have been selected as a simple illustration of Ascomycetes, but the group is a very

large one, and contains a great variety of forms. All of them, however, produce spores in asci, but the asci are not always inclosed by an ascocarp. Here belong the common blue mould (*Penicillium*), found on bread, fruit, etc., in which stage the branching chains of conidia are very conspicuous (Fig. 43); the truffle-fungi, upon whose subter-

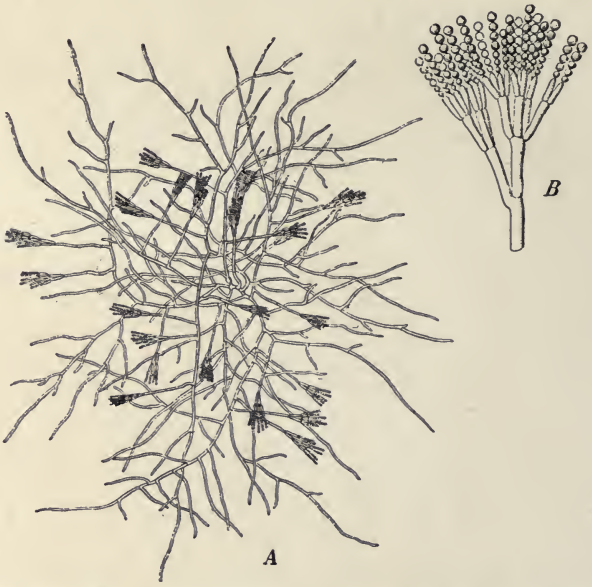


Fig. 43. *Penicillium*, a common mould: *A*, mycelium with numerous branching sporophores bearing conidia; *B*, apex of a sporophore enlarged, showing branching and chains of conidia.—After Brefeld.

ranean mycelia ascocarps develop which are known as "truffles"; the black fungi, which form the diseases known as "black knot" of the plum and cherry, the "ergot" of rye (Fig. 44), and many black wart-like growths upon the bark of trees; other forms causing "witches'-brooms" (abnormal growths on various trees), "peach curl," etc., the cup-fungi (Figs. 45, 46), and the edible morels (Fig. 47).

Fig. 44. Head of rye attacked by "ergot" (*a*), peculiar grain-like masses replacing the grains of rye; also a mass of "ergot" germinating to form spores (*b*).—After Tulasne.

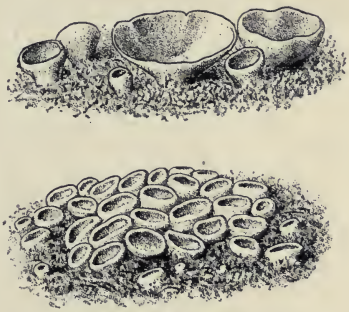


Fig. 45. Two species of cup-fungus (*Peziza*).—After Lindau.

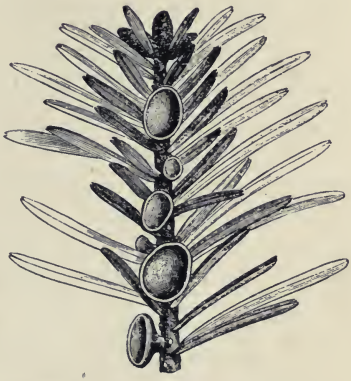


Fig. 46. A cup-fungus (*Pitya*) growing on a spruce (*Picea*).—After Rehm.

In some of these forms the ascocarp is completely closed, as in the lilac mildew; in others it is flask-shaped; in others, as in the cup-fungi, it is like a cup or disk; but in all the spores are inclosed by a delicate sac, the ascus.

Here must probably be included the yeast-fungi (Fig. 48), so commonly used to excite alcoholic fermentation.

FIG. 47. The common edible morel (*Morchella esculenta*). The structure shown and used represents the ascocarp, the depressions of whose surface are lined with asci containing ascospores.—After GIBSON.

FIG. 48. Yeast cells, reproducing by budding, and forming chains.—CALDWELL.

The "yeast cells" seem to be conidia having a peculiar budding method of multiplication, and the remarkable power of exciting alcoholic fermentation in sugary solutions.

3. ÆCIDIOMYCETES (*Æcidium-Fungi*)

45. **General characters.**—This is a large group of very destructive parasites known as "rusts" and "smuts." The rusts attack particularly the leaves of higher plants, producing rusty spots, the wheat rust probably being the best known. The smuts especially attack the grasses, and are very injurious to cereals, producing in the heads of oats, barley, wheat, corn, etc., the disease called smut.

No indication of a sexual process has been obtained, and the life histories are so complicated and obscure that the position of the group is very uncertain. The forms should probably be included with the Basidiomycetes, but they are so unlike the ordinary forms of that group that they are here kept distinct.

Most of the forms are very *polymorphic*—that is, a plant assumes several dissimilar appearances in the course of its life history. These phases are often so dissimilar that they have been described as different plants. This polymorphism is often further complicated by the appearance of different phases upon entirely different hosts. For example, the wheat-rust fungus in one stage lives on wheat, and in another on barberry.

46. **Wheat rust.**—This is one of the few rusts whose life histories have been traced, and it may be taken as an illustration of the group.

The mycelium of the fungus is found ramifying among the leaf and stem tissues of the wheat. While the wheat is growing this mycelium sends to the surface numerous spo-

Fig. 49. Wheat rust, showing sporophores breaking through the tissues of the host and bearing summer spores (uredospores).—After H. Marshall Ward.

rophores, each bearing at its apex a reddish spore (Fig. 49). As the spores occur in great numbers they form the rusty-looking lines and spots which give name to the disease. The spores are scattered by currents of air, and falling upon other plants, germinate very promptly, thus spreading the

disease with great rapidity (Fig. 50). Once it was thought that this completed the life cycle, and the fungus received the name *Uredo*. When it was known that this is but one

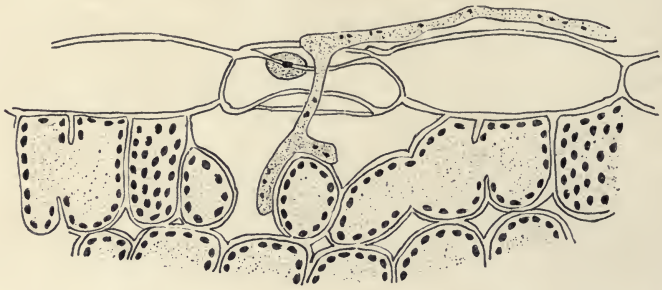


FIG. 50.—Wheat rust, showing a young hypha forcing its way from the surface of a leaf down among the nutritive cells.—After H. MARSHALL WARD.

stage in a polymorphic life history it was called the Uredo-stage, and the spores *uredospores*, sometimes "summer spores."

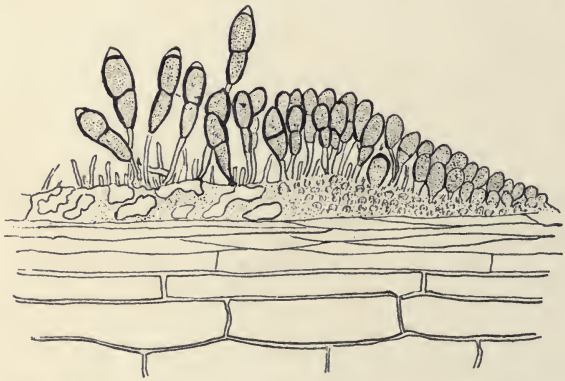


FIG. 51. Wheat rust, showing the winter spores (teleutospores).—After H. MARSHALL WARD.

Toward the end of the summer the same mycelium develops sporophores which bear an entirely different kind of spore (Fig. 51). It is two-celled, with a very heavy black

wall, and forms what is called the "black rust," which appears late in the summer on wheat stubble. These spores are the resting spores, which last through the winter and germinate in the following spring. They are called *teleutospores*, meaning the "last spores" of the growing season. They are also called "winter spores," to distinguish them from the uredospores or "summer spores." At first this teleutospore-bearing mycelium was not recognized to be identical with the uredospore-bearing mycelium, and it was called *Puccinia*. This name is now retained for the whole polymorphous plant, and wheat rust is *Puccinia graminis*. This mycelium on the wheat, with its summer spores and winter spores, is but one stage in the life history of wheat rust.

Fig. 52. Wheat rust, showing a teleutospore germinating and forming a short filament, from four of whose cells a spore branch arises, the lowest one bearing at its tip a sporidium.—After H. Marshall Ward.

In the spring the teleutospore germinates, each cell developing a small few-celled filament (Fig. 52). From each cell of the filament a little branch arises which develops at its tip a small spore, called a *sporidium*, which means "spore-like." This little filament, which is not a parasite, and which bears sporidia, is a second phase of the wheat rust, really the first phase of the growing season.

The sporidia are scattered, fall upon barberry leaves, germinate, and develop a mycelium which spreads through the leaf. This mycelium produces sporophores which emerge on the under surface of the leaf in the form of chains of reddish-yellow conidia (Fig. 53). These chains of conidia are closely packed in cup-like receptacles, and these reddish-yellow cup-like masses are often called

"cluster-cups." This mycelium on the barberry, bearing cluster-cups, was thought to be a distinct plant, and was called *Æcidium*. The name now is applied to the cluster-cups, which are called *æcidia*, and the conidia-like spores which they produce are known as *æcidiospores*.

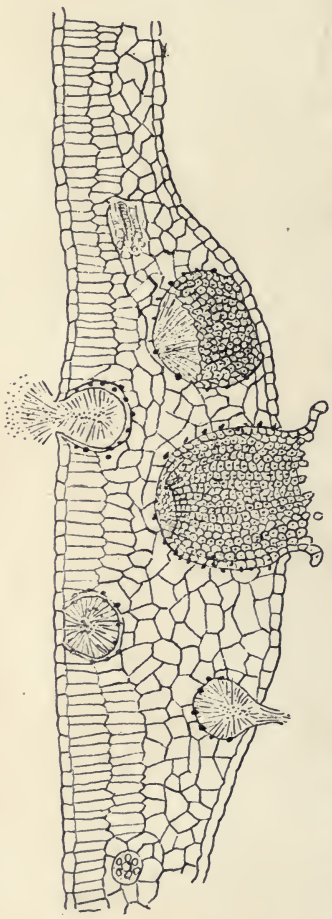


Fig. 53. Wheat rust, showing section of barberry leaf, with two æcidia below, one of them having broken through the epidermis and exposed its chains of conidia (æcidiospores). Above is a flask-shaped mass discharging very minute bodies, which are probably still other spores of the parasite.—After H. Marshall Ward.

It is the æcidia which give name to the group, and Æcidiomycetes are those Fungi in whose life history æcidia or cluster-cups appear.

The æcidiospores are scattered by the wind, fall upon the spring wheat, germinate, and develop again the mycelium which produces the rust on the wheat, and so the life cycle is completed. There are thus at least three distinct stages in the life history of wheat rust. Beginning with the growing season they are as follows: (1) The phase bearing the sporidia, which is not parasitic; (2) the æcidium phase, parasitic on the barberry; (3) the uredo-teleutospore phase, parasitic on the wheat.

In this life cycle at least four kinds of asexual spores

appear: (1) *sporidia*, which develop the stage on the barberry; (2) *œcidiospores*, which develop the stage on the wheat; (3) *uredospores*, which repeat the mycelium on the wheat; (4) *teleutospores*, which last through the winter, and in the spring produce the stage bearing sporidia. It should be said that there are other spores of this plant produced on the barberry (Fig. 53), but they are too uncertain to be included here.

The barberry is not absolutely necessary to this life cycle. In many cases there is no available barberry to act as host, and the sporidia germinate directly upon the young wheat, forming the rust-producing mycelium, and the cluster-cup stage is omitted.

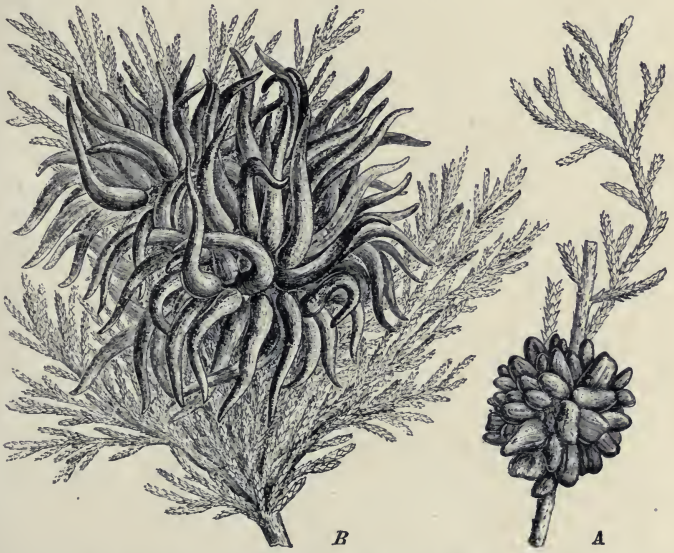


FIG. 54. Two species of "cedar apple" (*Gymnosporangium*), both on the common juniper (*Juniperus Virginiana*).—*A* after FARLOW, *B* after ENGLER and PRANTL.

47. **Other rusts.**—Many rusts have life histories similar to that of the wheat rust, in others one or more of the stages are omitted. In very few have the stages been con-

nected together, so that a mycelium bearing uredospores is called a *Uredo*, one bearing teleutospores a *Puccinia*, and one bearing æcidia an *Æcidium ;* but what forms of *Uredo*, *Puccinia*, and *Æcidium* belong together in the same life cycle is very difficult to discover.

Another life cycle which has been discovered is in connection with the "cedar apples" which appear on red cedar (Fig. 54). In the spring these diseased growths become conspicuous, especially after a rain, when the jelly-like masses containing the orange-colored spores swell. This corresponds to the phase which produces rust in wheat. On the leaves of apple trees, wild crab, hawthorn, etc., the æcidium stage of the same parasite develops.

4. Basidiomycetes (*Basidium-Fungi*).

48. **General characters.**—This group includes the mushrooms, toadstools, and puffballs. They are not destructive parasites, as are many forms in the preceding groups, but mostly harmless and often useful saprophytes. They must also be regarded as the most highly organized of the Fungi. The popular distinction between toadstools and mushrooms is not borne out by botanical characters, toadstool and mushroom being the same thing botanically, and forming one group, puffballs forming another.

Fig. 55. The common edible mushroom, *Agaricus campestris*.—After Gibson.

As in Æcidiomycetes, no sexual process has

been discovered. The life history seems simple, but this apparent simplicity may represent a very complicated history. The structure of the common mushroom (*Agaricus*) will serve as an illustration of the group (Fig. 55).

49. **A common mushroom.** — The mycelium, of white branching threads, spreads extensively through the decaying substratum, and in cultivated forms is spoken of as the "spawn." Upon this mycelium little knob-like protuberances begin to arise, growing larger and larger, until they are organized into the so-called "mushrooms." The real body of the plant is the white thread-like mycelium, while the "mushroom" part seems to represent a great number of sporophores organized together to form a single complex spore-bearing structure.

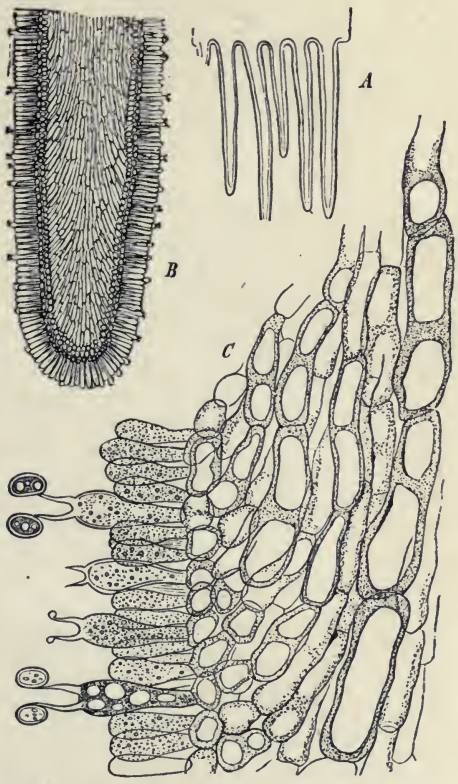


FIG. 56. A common *Agaricus*: *A*, section through one side of pileus, showing sections of the pendent gills; *B*, section of a gill more enlarged, showing the central tissue, and the broad border formed by the basidia: *C*, still more enlarged section of one side of a gill, showing the club-shaped basidia standing at right angles to the surface, and sending out a pair of small branches, each of which bears a single basidiospore.—After SACHS.

The mushroom

FIG. 57. A "fairy ring" fungus (*Marasmius oreades*); edible.—After GIBSON.

FIG. 58. A common poisonous toadstool (*Amanita*), showing stipe, pileus, and gills.—CALDWELL.

FIG. 59. The "shaggy mane" fungus (*Coprinus comatus*); edible.—After GIBSON.

has a stalk-like portion, the *stipe*, at the base of which the slender mycelial threads look like white rootlets; and an expanded, umbrella-like top called the *pileus*. From the under surface of the pileus there hang thin radiating plates, or *gills* (Fig. 55). Each gill is a mass of interwoven filaments (hyphæ), whose tips turn toward the surface and form a compact layer of end cells (Fig. 56). These end

FIG. 60. A bracket fungus (*Polyporus*) growing on the trunk of a red oak.—CALDWELL.

cells, forming the surface of the gill, are club-shaped, and are called *basidia*. From the broad end of each basidium two or four delicate branches arise, each bearing a minute spore, very much as the sporidia appear in the wheat rust.

These spores, called *basidiospores*, shower down from the gills when ripe, germinate, and produce new mycelia. The peculiar cell called the basidium gives name to the group Basidiomycetes.

50. **Other forms.**—Mushrooms display a great variety of form and coloration, many of them being very attractive

Fig. 61. A toadstool of the bracket form which has grown about blades of grass without interfering with their activity.—Caldwell.

(Figs. 57, 58, 59). The "pore-fungi" have pore-like depressions for their spores, instead of gills, as in the very common "bracket-fungus" (*Polyporus*), which forms hard shell-like outgrowths on tree-trunks and stumps (Figs. 60,

Fig. 62. The common edible *Boletus* (*B. edulis*), in which the gills are replaced by pores.—After Gibson.

Fig. 63. Another edible *Boletus* (*B. strobilaceus*).—After Gibson.

Fig. 64. The common edible "coral fungus" (*Clavaria*).—After Gibson.

Fig. 65. *Hydrum repandum*, in which gills are replaced by spinous processes; edible.—After Gibson.

61), and the mushroom-like *Boleti* (Figs. 62, 63). The "ear-fungi" form gelatinous, dark-brown, shell-shaped masses, and the "coral fungi" resemble branching corals (Fig. 64). The Hydnum forms have spinous processes instead of gills (Fig. 65). The puffballs organize globular bodies (Fig. 66), within which the spores develop, and are not liberated until ripe; and with them belong also the "bird's nest fungus," the "earth star," the ill-smelling "stink-horn," etc.

Fig. 66. Puffballs, in which the basidia and spores are inclosed; edible.—After Gibson.

OTHER THALLOPHYTES WITHOUT CHLOROPHYLL

51. **Slime-moulds.** — These perplexing forms, named *Myxomycetes*, do not seem to be related to any group of plants, and it is a question whether they are to be regarded as plants or animals. The working body is a mass of naked protoplasm called a *plasmodium*, suggesting the term "slime," and slips along like a gigantic amœba. They are common in forests, upon black soil, fallen leaves, and decaying logs, the slimy yellow or orange masses ranging from the size of a pinhead to as large as a man's hand. They are saprophytic, and are said to engulf food as do the amœbas. So suggestive of certain low animals is this body and food habit that slime-moulds have also been called *Mycetozoa* or "fungus-animals."

In certain conditions, however, these slimy bodies come to rest and organize most elaborate and often very beautiful sporangia, full of spores (Fig. 67). These varied and easily preserved sporangia are used to classify the

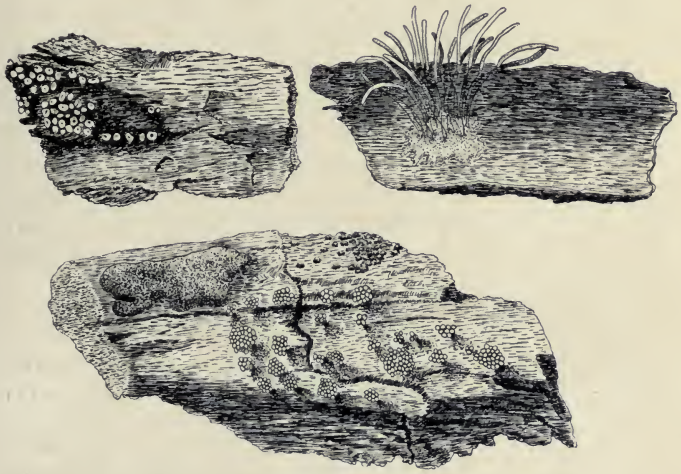


Fig. 67. Three common slime moulds (Myxomycetes) on decaying wood: to the left above, groups of the sessile sporangia of *Trichia*; to the right above, a group of the stalked sporangia of *Stemonitis*, with remnant of old plasmodium at base; below, groups of sporangia of *Hemiarcyria*, with a plasmodium mass at upper left hand.—Caldwell.

forms. Slime-moulds, or "slime-fungi," therefore, seem to have animal-like bodies which produce plant-like sporangia.

52. **Bacteria.**—These are the "Fission-Fungi," or Schizomycetes, and are popularly known as "bacteria," "bacilli," "microbes," "germs," etc. They are so important and peculiar in their life habits that their study has developed a special branch of botany, known as "Bacteriology." In many ways they resemble the Cyanophyceæ, or "Fission-Algæ," so closely that they are often associated with them in classification (see § 21).

FIG. 68. A group of Bacteria, the bodies being black, and bearing motile cilia in various ways. *A*, the two to the left the common hay *Bacillus* (*B. subtilis*), the one to the right a *Spirillum*; *B*, a Coccus form (*Planococcus*); *C*, *D*, *E*, species of *Pseudomonas*; *F*, *G*, species of Bacillus, *F* being that of typhoid fever; *H*, *Microspira*; *J*, *K*, *L*, *M*, species of *Spirillum*.—After ENGLER and PRANTL.

They are the smallest known living organisms, the one-celled form which develops on cooked potatoes, bread, milk, meat, etc., forming a blood-red stain, having a diameter of but 0.0005 mm. ($\frac{1}{50000}$ in.). They are of various forms (Fig. 68), as Coccus forms, single spherical cells; Bacterium forms, short rod-shaped cells; Bacillus forms, longer rod-shaped cells; Leptothrix forms, simple filaments; Spirillum forms, spiral filaments, etc.

They multiply by cell division with wonderful rapidity, and also form resting spores for preservation and distribution. They occur everywhere—in the air, in the water, in the soil, in the bodies of plants and animals; many of them harmless, many of them useful, many of them dangerous.

They are intimately concerned with fermentation and decay, inducing such changes as the souring of fruit juices, milk, etc., and the development of pus in wounds. What is called antiseptic surgery is the use of various means to exclude bacteria and so prevent inflammation and decay.

The pathogenic forms—that is, those which induce diseases of plants and animals—are of great importance, and means of making them harmless or destroying them are being searched for constantly. They are the causes of such diseases as pear-blight and peach-yellows among plants, and such human diseases as tuberculosis, cholera, diphtheria, typhoid fever, etc.

LICHENS

53. **General character.** — Lichens are abundant everywhere, forming various colored splotches on tree-trunks, rocks, old boards, etc., and growing also upon the ground (Figs. 69, 70, 71). They have a general greenish-gray color, but brighter colors may also be observed.

The great interest connected with Lichens is that they are not single plants, but each Lichen is formed of a fungus and an alga, living together so intimately as to appear like a single

FIG. 69. A ledge of rock, showing the face to the right covered by a dense growth of lichens, and on top a growth of ferns (*Cystopteris bulbifera*). Near Deer Park, Ill.—CALDWELL.

plant. In other words, a Lichen is not an individual, but a firm of two individuals very unlike each other. This habit

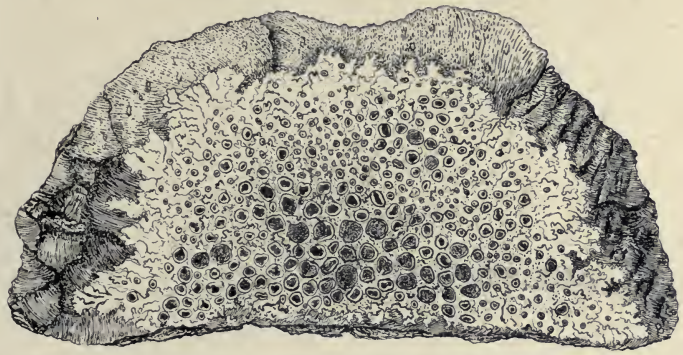


FIG. 70. A common lichen (*Physcia*) growing on bark, showing the spreading thallus and the numerous dark disks (apothecia) bearing the asci.—CALDWELL.

of living together has been called *symbiosis*, and the individuals entering into this relation are called *symbionts*.

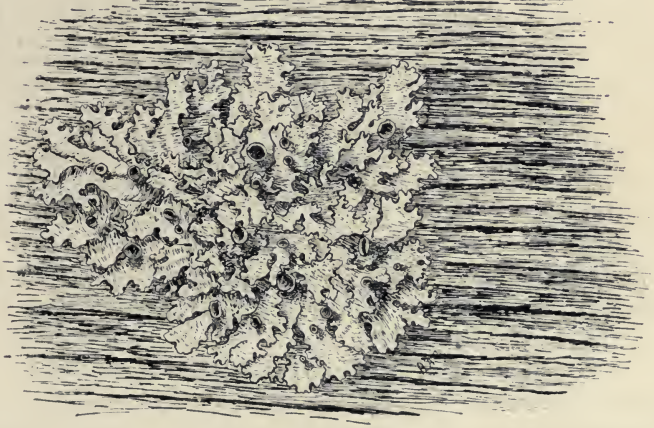


FIG. 71. A common foliose lichen (*Parmelia*) growing upon a board, and showing apothecia.—CALDWELL.

If a Lichen be sectioned, the relation between the symbionts will be seen (Fig. 72). The fungus makes the bulk of the body with its interwoven mycelial threads, in the meshes of which lie the Algæ, sometimes scattered, some-

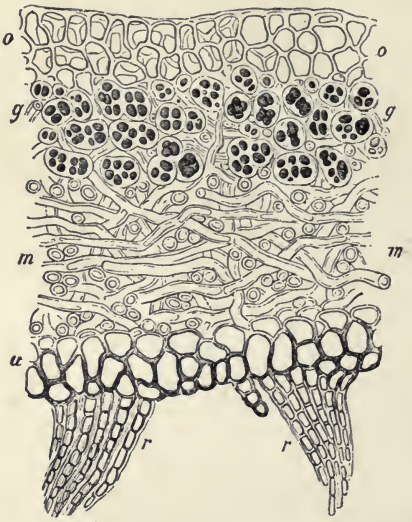


Fig. 72. Section through thallus of a lichen (*Sticta*), showing holdfasts (*r*), lower (*u*) and upper (*o*) surfaces, fungus hyphæ (*m*), and enmeshed algæ (*g*).—After Sachs.

times massed. It is these enmeshed Algæ, showing through the transparent mycelium, that give the greenish tint to the Lichen.

In the case of Lichens the symbionts are thought by some to be mutually helpful, the alga manufacturing food for the fungus, and the fungus providing protection and water containing food materials for the alga. Others do not recognize any special benefit to the alga, and see in a Lichen simply a parasitic fungus living on the products of an alga. In any event the Algæ are not destroyed but seem to thrive. It is discovered that the alga symbiont can live quite inde-

pendently of the fungus. In fact, the enmeshed Algæ are often recognized as identical with forms living independently, those thus used being various Blue-green, Protococcus, and Conferva forms.

On the other hand, the fungus symbiont has become quite dependent upon the alga, and its germinating spores do not develop far unless the young mycelium can lay hold of suitable Algæ. At certain times cup-like or disk-like bodies appear on the surface of the lichen thallus, with brown, or black, or more brightly-colored lining (Figs. 70, 71). These bodies are the *apothecia*, and a section through them shows that the colored lining is largely made up of delicate sacs containing spores (Figs. 73, 74). These sacs are evidently asci, the apothecia correspond to ascocarps, and the Lichen fungus proves to be an Ascomycete.

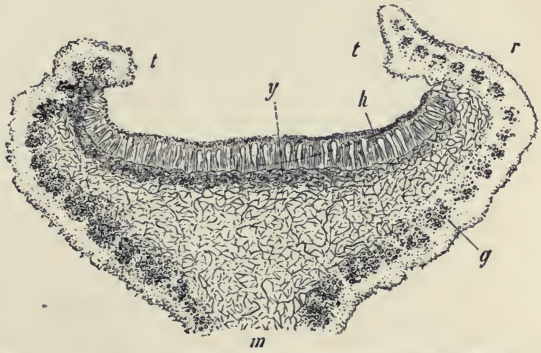


FIG. 73. Section through an apothecium of *Anaptychia*, showing stalk of the cup (*m*), masses of algal cells (*g*), outer margin of cup (*r*), overlapping edge (*t. t*), layer of asci (*h*), and massing of hyphæ beneath asci (*y*).—After SACHS.

Certain Ascomycetes, therefore, have learned to use certain Algæ in this peculiar way, and a Lichen is the result. Some Basidiomycetes have also learned the same habit, and form Lichens.

Various forms of Lichen bodies can be distinguished as follows: (1) *Crustaceous Lichens*, in which the thallus resem-

bles an incrustation upon its substratum of rock, soil, etc.; (2) *Foliose Lichens*, with flattened, leaf-like, lobed bodies, at-

Fig. 74. Much enlarged section of a portion of the apothecium of *Anaptychia*, showing the fungus mycelium (*m*), which is massed above (*y*), just beneath the layer of asci (*1*, *2*, *3*, *4*), in which spores in various stages of development are shown.—After Sachs.

tached only at the middle or irregularly to the substratum; (3) *Fruticose Lichens*, with filamentous bodies branching like shrubs, either erect, pendulous, or prostrate.

CHAPTER VI

THE FOOD OF PLANTS

54. **Introductory.**—All plants use the same kind of food, but the Algæ and Fungi suggest that they may have very different ways of obtaining it. The Algæ can manufacture food from raw material, while the Fungi must obtain it already manufactured. Between these two extreme conditions there are plants which can manufacture food, and at the same time have formed the habit of supplementing this by obtaining elsewhere more or less manufactured food. Besides this, there are plants which have learned to work together in the matter of food supply, entering into a condition of symbiosis, as described under the Lichens. These various habits will be presented here briefly.

55. **Green plants.**—The presence of chlorophyll enables plants to utilize carbon dioxide (CO_2), a gas present in the atmosphere and dissolved in waters, and one of the waste products given off in the respiration of all living organisms. This gas is absorbed by green plants, its constituent elements, carbon and oxygen, are dissociated, and with the elements obtained from absorbed water (H_2O) are recombined to form a carbohydrate (sugar, starch, etc.), which is an organized food. With this as a basis other foods are formed, and so the plant can live without help from any other organism.

This process of utilizing carbon dioxide in the formation of food is not only a wonderful one, but also very important. It is wonderful, because carbon dioxide and water, both of them very refractory substances, are broken up at ordinary

temperatures and without any special display of energy. It is important, because the food of all plants and animals depends upon it, as it is the only known process by which inorganic material can be organized.

The process is called *photosynthesis*, or *photosyntax*, words indicating that the presence of light is necessary. The mechanism on the part of the plant is the chloroplast, which when exposed to light is able to do this work. The process is often called " carbon assimilation," " chlorophyll assimilation," " fixation of carbon," etc. It should be noted that it is not the chlorophyll which does the work, but the protoplasmic plastid stained green by the chlorophyll. The chlorophyll manipulates the light in some way so that the plastid may obtain from it the energy needed for the work. Further details concerning it may be obtained by reading § 112 of *Plant Relations.*

It is evident that green plants must expose their chlorophyll to the light. For this reason the Algæ can not live in deep waters or in dark places. In the case of the large marine kelps, although they may be anchored in considerable depth of water, their working bodies are floated up toward the light by air-bladders. In the case of higher plants, specially organized chlorophyll-bearing organs, the foliage leaves, are developed.

56. **Saprophytes.**—Only cells containing chloroplasts can live independently. In the higher plants, where bodies become large, many living cells are shut away from the light, and must depend upon the more superficial green cells for their food supply. The habit of cells depending upon one another for food, therefore, is a very common one.

When none of the cells of the plant body contain chlorophyll, the whole plant becomes dependent, and must live as a saprophyte or a parasite. In the case of saprophytes dead bodies or body products are attacked, and sooner or later all organic matter is attacked and decomposed by them. The decomposition is a result of the nutritive processes of plants

without chlorophyll, and were it not for them "the whole surface of the earth would be covered with a thick deposit of the animal and plant remains of the past thousands of years."

The green plants, therefore, are the manufacturers of organic material, producing far more than they can use, while the plants without chlorophyll are the destroyers of organic material. The chief destroyers are the Bacteria and ordinary Fungi, but some of the higher plants have also adopted this method of obtaining food. Many ordinary green plants have the saprophytic habit of absorbing organic material from rich humus soil; and many orchids and heaths are parasitic, attaching their subterranean parts to those of other plants, becoming what are called "root parasites." The cultivated plants, also, may be regarded as partially saprophytic, in so far as they use the organic material supplied to them in fertilizers.

57. **Parasites.**—Certain plants without chlorophyll are not content to obtain organic material from dead bodies, but attack living ones. As in the case of saprophytes, the vast majority of plants which have formed this habit are Bacteria and ordinary Fungi. Parasites are not only modified in structure in consequence of the absence of chlorophyll, but they have developed means of penetrating their hosts. Many of them have also cultivated a very selective habit, restricting themselves to certain plants or animals, or even to certain organs.

The parasitic habit has also been developed by some of the higher plants, sometimes completely, sometimes partially. Dodder, for example, is completely parasitic at maturity (Fig. 75), while mistletoe is only partially so, doing chlorophyll work and also absorbing from the tree into which it has sent its haustoria.

That saprophytism and parasitism are both habits gradually acquired is inferred from the number of green plants which have developed them more or less, as a supplement to

the food which they manufacture. The less chlorophyll is used the less is it developed, and a green plant which is obtaining the larger amount of its food in a saprophytic or parasitic way is on the way to losing all of its chlorophyll and becoming a complete saprophyte or parasite.

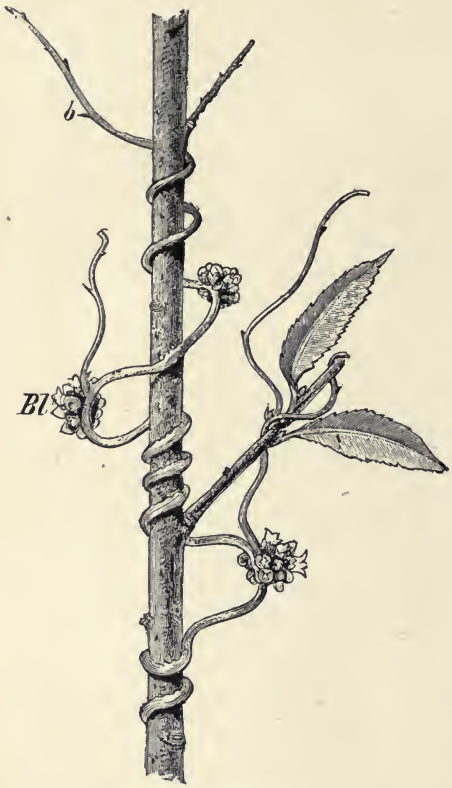


FIG. 75. A dodder plant parasitic on a willow twig. The leafless dodder twines about the willow, and sends out sucking processes which penetrate and absorb.—After STRASBURGER.

Certain of the lower Algæ are in the habit of living in the body cavities of higher plants, finding in such situations the moisture and protection which they need. They may thus have brought within their reach some of the organic products of the higher plant. If they can use some of these, as is very likely, a partially parasitic habit is begun, which may lead to loss of chlorophyll and complete parasitism.

58. **Symbionts.** — The phenomenon of symbiosis has already been referred to in connection with Lichens (§ 53). In its broadest sense the word includes any sort of dependence between living organisms, from the vine and the tree

upon which it climbs, to the alga and fungus so intimately associated in a Lichen as to seem a single plant. In a narrower sense it includes only cases in which there is an intimate organic relation between the symbionts. This would include parasitism, the parasite and host being the symbionts, and the organic relation certainly being intimate. In a still narrower sense symbiosis includes only those cases in which the symbionts are mutually helpful. This fact, however, is very difficult to determine, and opinions vary widely as to the mutual advantage of the relation. However large a set of phenomena may be included under the term symbiosis, we use it here in this narrowest sense, which is often distinguished as *mutualism*.

(1) *Lichens.*—The main facts of symbiosis in connection with Lichens were presented in § 53. That the fungus-symbiont can not live without the alga has been demonstrated, but whether the alga-symbiont derives any benefit from this association is a question in dispute. The latter can live independently of the former, but enmeshed by the fungus the alga seems to thrive and to live in situations which would be impossible to it without the protection and moisture supplied by the fungus-thallus. Those who lay stress on the first fact regard the Lichen merely as a peculiar case of parasitism, which has been called *helotism*, or a condition of slavery, indicating that the alga is enslaved and even cared for by the fungus for its own use. Those who see an advantage to the alga in this association regard a Lichen as an example of mutualism.

It may be of interest to know that artificial Lichens have been formed, not only by cultivating together spores of a Lichen-fungus and some Lichen-alga, but also by using "wild" Algæ—that is, Algæ which are in the habit of living independently.

(2) *Mycorrhiza.*—The name means "root-fungus," and refers to an association which exists between certain Fungi of the soil and roots of higher plants, such as orchids, heaths,

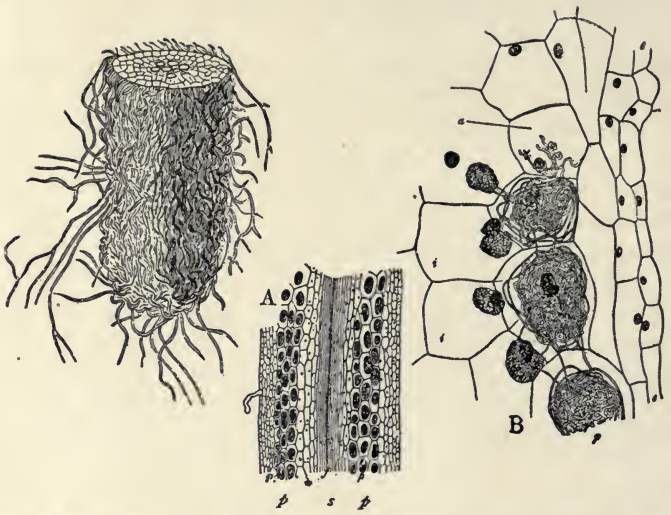


Fig. 76. Mycorrhiza: to the left is the tip of a rootlet of beech enmeshed by the fungus; *A*, diagram of longitudinal section of an orchid root, showing the cells of the cortex (*p*) filled with hyphæ; *B*, part of longitudinal section of orchid root much enlarged, showing epidermis (*e*), outermost cells of the cortex (*p*) filled with hyphal threads, which are sending branches into the adjacent cortical cells (*a*, *i*). —After Frank.

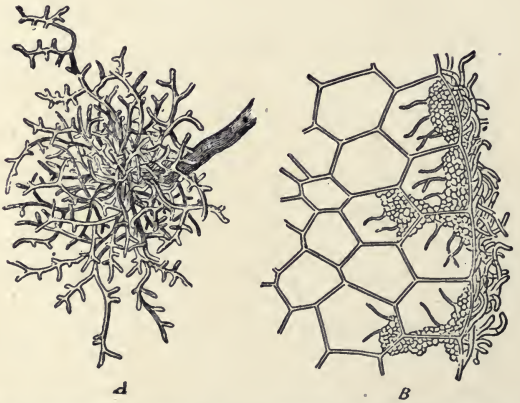


Fig. 77. Mycorrhiza: *A*, rootlets of white poplar forming mycorrhiza; *B*, enlarged section of single rootlets, showing the hyphæ penetrating the cells.—After Kerner.

oaks and their allies, etc. (Figs. 76, 77). The delicate branching filaments (hyphæ) of the fungus spread through the soil, wrap the rootlets with a mesh of hyphæ, and penetrate into the cells. It seems clear that the fungus obtains food from the rootlet as a parasite; but it is also thought that the hyphal threads, spreading widely through the soil, are of great service to the host plant in aiding the rootlets in absorbing. If this be true, there is mutual advantage in the association, for the small amount of nourishment taken by the fungus is more than compensated by its assistance in absorption.

(3) *Root-tubercles.*—On the roots of many legume plants, as clovers, peas, beans, etc., little wart-like outgrowths are frequently found, known as "root-tubercles" (Fig. 78). It is found that these tubercles are caused by certain Bacteria, which penetrate the roots and induce these excrescent growths. The tubercles are found to swarm with Bacteria, which are doubtless obtaining food from the roots of the host. At the same time, these Bacteria have the peculiar power of laying hold of the free nitrogen of the air circulating in the soil, and of supplying it to the host plant in some usable form. Ordinarily plants can not use free nitrogen, although it occurs in the air in such abundance, and this power of these soil Bacteria is peculiarly interesting.

FIG. 78. Root-tubercles on *Vicia Faba.*—After NOLL.

This habit of clover and its allies explains why they are useful in what is called "restoring the soil." After ordi-

nary crops have exhausted the soil of its nitrogen-containing salts, and it has become comparatively sterile, clover is able to grow by obtaining nitrogen from the air through the root-tubercles. If the crop of clover be "plowed under," nitrogen-containing materials which the clover has organized will be contributed to the soil, which is thus restored to a condition which will support the ordinary crops again. This indicates the significance of a very ordinary "rotation of crops."

(4) *Ant-plants, etc.*—In symbiosis one of the symbionts may be an animal. Certain fresh-water polyps and sponges become green on account of Algæ which they harbor within their bodies (Fig. 79). Like the Lichen-fungus, these animals use the food manufactured by the Algæ, which in turn find a congenial situation for living. By some this would also be regarded as a case of helotism, the animal enslaving the alga.

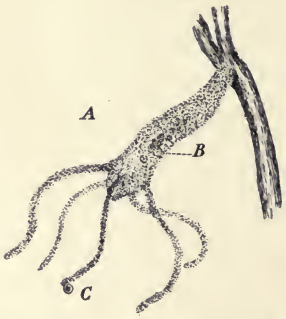


FIG. 79. A fresh-water polyp (*Hydra*) attached to a twig and feeding upon algæ (*C*), which may be seen through the transparent body wall (*B*).—CALDWELL.

Very definite arrangements are made by certain plants for harboring ants, which in turn guard them against the attack of leaf-cutting insects and other foes. These plants are called *Myrmecophytes*, which means "ant-plants," or *myrmecophilous plants*, which means "plants loving ants." These plants are mainly in the tropics, and in stem cavities, in hollow thorns, or elsewhere, they provide dwelling places for tribes of warlike ants (Fig. 80). In addition to these dwelling places they provide special kinds of food for the ants.

(5) *Flowers and insects.*—A very interesting and important case of symbiosis is that existing between flowers and insects. The flowers furnish food to the insects, and the

latter are used by the flowers as agents of pollination. An account of this relationship is deferred until seed-plants are

FIG. 80. An ant plant (*Hydnophytum*) from South Java, in which an excrescent growth provides a habitation for ants.—After SCHIMPER.

considered, or it may be found, with illustrations, in *Plant Relations*, Chapter VII.

59. **Carnivorous plants.**—Certain green plants, growing in situations poor in nitrogen-containing salts, have learned to supplement the proteids which they manufacture by capturing and digesting insects. The various devices employed for securing insects have excited great interest, since they do not seem to be associated with the ordinary idea of plant activities. Prominent among these forms are the bladderworts, pitcher-plants, sundews, Venus's fly-trap, etc. For further account and illustrations of these plants see *Plant Relations*, § 119.

CHAPTER VII

BRYOPHYTES (MOSS PLANTS)

60. **Summary from Thallophytes.**—Before considering the second great division of plants it is well to recall the most important facts connected with the Thallophytes, those things which may be regarded as the contribution of the Thallophytes to the evolution of the plant kingdom, and which are in the background when one enters the region of the Bryophytes.

(1) *Increasing complexity of the body.*—Beginning with single isolated cells, the plant body attains considerable complexity, in the form of simple or branching filaments, cell-plates, and cell-masses.

(2) *Appearance of spores.*—The setting apart of reproductive cells, known as spores, as distinct from nutritive cells, and of reproductive organs to organize these spores, represents the first important differentiation of the plant body into nutritive and reproductive regions.

(3) *Differentiation of spores.*—After the introduction of spores they become different in their mode of origin, but not in their power. The asexual spore, ordinarily formed by cell division, is followed by the appearance of the sexual spore, formed by cell union, the act of cell union being known as the sexual process.

(4) *Differentiation of gametes.*—At the first appearance of sex the sexual cells or gametes are alike, but afterward they become different in size and activity, the large passive one being called the egg, the small active one the

sperm, the organs producing the two being known as oogonium and antheridium respectively.

(5) *Algæ the main line.*—The Algæ, aquatic in habit, appear to be the Thallophytes which lead to the Bryophytes and higher groups, the Fungi being regarded as their degenerate descendants; and among the Algæ the Chlorophyceæ seem to be most probable ancestors of higher forms. It should be remembered that among these Green Algæ the ciliated swimming spore (zoospore) is the characteristic asexual spore, and the sexual spore (zygote or oospore) is the resting stage of the plant, to carry it over from one growing season to the next.

61. **General characters of Bryophytes.**—The name given to the group means "moss plants," and the Mosses may be regarded as the most representative forms. Associated with them in the group, however, are the Liverworts, and these two groups are plainly distinguished from the Thallophytes below, and from the Pteridophytes above. Starting with the structures that the Algæ have worked out, the Bryophytes modify them still further, and make their own contributions to the evolution of the plant kingdom, so that Bryophytes become much more complex than Thallophytes.

62. **Alternation of generations.**—Probably the most important fact connected with the Bryophytes is the distinct alternation of generations which they exhibit. So important is this fact in connection with the development of the plant kingdom that its general nature must be clearly understood. Probably the clearest definition may be obtained by tracing in bare outline the life history of an ordinary moss.

Beginning with the asexual spore, which is not ciliated, as there is no water in which it can swim, we may imagine that it has been carried by the wind to some spot suitable for its germination. It develops a branching filamentous growth which resembles some of the Conferva forms among the Green Algæ (Fig. 81). It is prostrate, and is a regu-

lar thallus body, not at all resembling the "moss plant" of ordinary observation, and is not noticed by those unaware of its existence.

Presently one or more buds appear on the sides of this alga-like body (Fig. 81, *b*). A bud develops into an erect

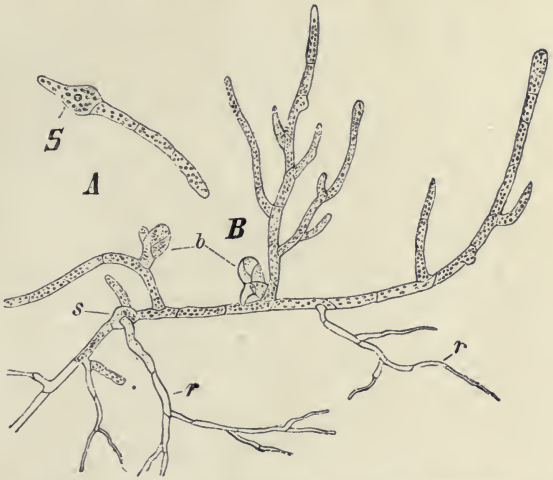


FIG. 81. Protonema of moss: *A*, very young protonema, showing spore (*S*) which has germinated it; *B*, older protonema, showing branching habit, remains of spore (*s*), rhizoids (*r*), and buds (*b*) of leafy branches (gametophores).—After MÜLLER and THURGAU.

stalk upon which are numerous small leaves (Figs. 82, 102). This leafy stalk is the "moss plant" of ordinary observation, and it will be noticed that it is simply an erect leafy branch from the prostrate alga-like body.

At the top of this leafy branch sex-organs appear, corresponding to the antheridia and oogonia of the Algæ, and within them there are sperms and eggs. A sperm and egg fuse and an oospore is formed at the summit of the leafy branch.

The oospore is not a resting spore, but germinates immediately, forming a structure entirely unlike the moss

FIG. 82. A common moss (*Polytrichum commune*), showing the leafy gametophore with rhizoids (*rh*), and two sporophytes (sporogonia), with seta (*s*), calyptra (*c*), and operculum (*d*), the calyptra having been removed.—After SCHENCK.

plant from which it came. This new leafy body consists of a slender stalk bearing at its summit an urn-like case in which are developed numerous asexual spores (Figs. 82, 107). This whole structure is often called the "spore fruit," and its stalk is imbedded at base in the summit of the leafy branch, thus obtaining firm anchorage and absorbing what nourishment it needs, but no more a part of the leafy branch than is a parasite a part of the host.

When the asexual spores, produced by the "spore fruit," germinate, they reproduce the alga-like body with which we began, and the life cycle is completed.

In examining this life history, it is apparent that each spore produces a different structure. The asexual spore produces the alga-like body with its erect leafy branch, while the oospore produces the "spore fruit" with its leafless stalk and spore case. These two structures, one produced by the asexual spore, the other by the oospore, appear in alternating succession, and this is what is meant by *alternation of generations*.

These two "generations" differ strikingly from one another in the spores which they produce. The generation composed of alga-like body and erect leafy branch pro-

duces only sexual spores (oospores), and therefore produces sex organs and gametes. It is known, therefore, as the *gametophyte*—that is, "the gamete plant."

The generation which consists of the "spore fruit"—that is, leafless stalk and spore case—produces only asexual spores, and is called the *sporophyte*—that is, "the spore plant."

Alternation of generations, therefore, means the alternation of a gametophyte and a sporophyte in completing a life history. Instead of having the same body produce both asexual and sexual spores, as in most of the Algæ, the two kinds of spores are separated upon different structures, known as "generations." It is evident that the gametophyte is the sexual generation, and the sporophyte the asexual one; and it should be kept clearly in mind that the asexual spore always produces the gametophyte, and the sexual spore the sporophyte. In other words, each spore produces not its own generation, but the other one.

The relation between the two alternating generations may be indicated clearly by the following formula, in which G and S are used for gametophyte and sporophyte respectively:

$$G \rightleftharpoons^{o}_{o} > o—S—o—G \rightleftharpoons^{o}_{o} > o—S—o—G, \text{ etc.}$$

The formula indicates that the gametophyte produces two gametes (sperm and egg), which fuse to form an oospore, which produces the sporophyte, which produces an asexual spore, which produces a gametophyte, etc.

That alternation of generations is of great advantage is evidenced by the fact that it appears in all higher plants. It must not be supposed that it appears first in the Bryophytes, for its beginnings may be seen among the Thallophytes. The Bryophytes, however, first display it fully organized and without exception. Just what this alternation does for plants may not be fully known, but one advantage seems prominent. By means of it many gametophytes may result from a single oospore; in other words,

it multiplies the product of the sexual spore. A glance at the formula given above shows that if there were no sporophyte (S) the oospore would produce but one gametophyte (G). By introducing the sporophyte, however, as many gametophytes may result from a single oospore as there are asexual spores produced by the sporophyte, which usually produces a very great number.

In reference to the sporophytes and gametophytes of Bryophytes two peculiarities may be mentioned at this point: (1) the sporophyte is dependent upon the gametophyte for its nourishment, and remains attached to it; (2) the gametophyte is the special chlorophyll-generation, and hence is the more conspicuous. It follows that, in a general way, the sporophyte of the Bryophytes only produces spores, while the gametophyte both produces gametes and does chlorophyll work.

It is important also to note that the protected resting stage in the life history is not the sexual spore, as in the Algæ, but is the asexual spore in connection with the sporophyte. These spores have a protecting wall, are scattered, and may remain for some time without germination.

If the ordinary terms in reference to Mosses be fitted to the facts given above, it is evident that the "moss plant" is the leafy branch of the gametophyte; that the "moss fruit" is the sporophyte; and that the alga-like part of the gametophyte has escaped attention and a name.

The names now given to the different structures which appear in this life history are as follows: The alga-like part of the gametophyte is the *protonema*, the leafy branch is the *gametophore* ("gamete-bearer"); the whole sporophyte is the *sporogonium* (a name given to this peculiar leafless sporophyte of Bryophytes), the stalk-like portion is the *seta*, the part of it imbedded in the gametophore is the *foot*, and the urn-like spore-case is the *capsule*.

63. **The antheridium.**—The male organ of the Bryophytes is called an antheridium, just as among Thallophytes, but it has a very different structure. In general among the

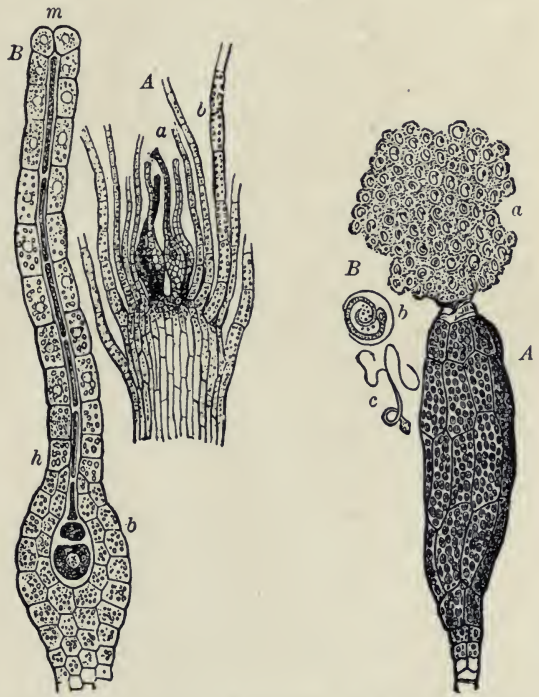


FIG. 83. Sex organs of a common moss (*Funaria*): the group to the right represents an antheridium (*A*) discharging from its apex a mass of sperm mother cells (*a*), a single mother cell with its sperm (*b*), and a single sperm (*c*), showing body and two cilia; the group to the left represents an archegonial cluster at summit of stem (*A*), showing archegonia (*a*), and paraphyses and leaf sections (*b*), and also a single archegonium (*B*), with venter (*b*) containing egg and ventral canal cell, and neck (*h*) containing the disorganizing axial row (neck canal cells).—After SACHS.

Thallophytes it is a single cell (mother cell), and may be called a simple antheridium, but in the Bryophytes it is a many-celled organ, and may be regarded as a compound antheridium. It is usually a stalked, club-shaped, or oval to

globular body (Figs. 83, 84, 103). A section through this body shows it to consist of a single layer of cells, which forms the wall of the antheridium, and within this a compact mass of small cubical (square in section) cells, within each one of which there is formed a single sperm (Fig. 84).

Fig. 84. Antheridium of a liverwort in section, showing single layer of wall cells surrounding the mass of mother cells.—After Strasburger.

These cubical cells are evidently mother cells, and to distinguish them from others they are called *sperm mother cells.* An antheridium, therefore, aside from its stalk, is a mass of sperm mother cells surrounded by a wall consisting of one layer of cells.

The sperm is a very small cell with two long cilia (Fig. 83). The two parts are spoken of as "body" and cilia, and the body may be straight or somewhat curved. These small biciliate sperms are one of the distinguishing marks of the Bryophytes. The existence of male gametes in the form of ciliated sperms indicates that fertilization can take place only in the presence of water, so that while the plant has become terrestrial, and its asexual spores have responded to the new conditions and are no longer ciliated, its sexual process is conducted as among the Green Algæ. It must not be supposed, however, that any great amount of water is necessary to enable sperms to swim, even a film of dew often answering the purpose.

When the mature antheridia are wet they are ruptured at the apex and discharge the mother cells in a mass (Figs. 83, 105, *E*), the walls of the mother cells become mucilaginous, and the sperms escaping swim actively about and are attracted to the organ containing the egg.

64. **The archegonium.**—This name is given to the female sex organ, and it is very different from the oogonium of

Thallophytes. Instead of being a single mother cell, it is a many-celled structure, shaped like a flask (Figs. 83, 98). The neck of the flask is more or less elongated, and within the bulbous base (*venter*) the single egg is organized. The archegonium, made up of neck and venter, consists mostly of a single layer of cells. This hollow flask is solid at first, there being a central vertical row of cells surrounded by the single layer just referred to. All of the cells of this axial row, except the lowest one, disorganize and leave a passageway down through the neck. The lowest one of the row, which lies in the venter of the archegonium, organizes the egg. In this way there is formed in the archegonium an open passageway through the neck to the egg lying in the venter.

To this neck the swimming sperms are attracted, enter and pass down it, one of them fuses with the egg, and this act of fertilization results in an oospore.

It is supposed that archegonia have been derived in some way from oogonia, but no intermediate stages suggest the steps. In any event, the presence of the archegonia is one strong and unvarying distinction between Thallophytes and Bryophytes. Pteridophytes also have archegonia, and so characteristic an organ is it that Bryophytes and Pteridophytes are spoken of together as *Archegoniates*.

65. **Germination of the oospore.**—The oospore in Bryophytes is not a resting spore, but germinates immediately by cell division, forming the sporophyte embryo, which presently develops into the mature sporophyte (Fig. 85, *A*). The lower part of the embryo develops downward into the gametophore, forming the foot, which penetrates and obtains a firm anchorage in the gametophore (Fig. 85, *B*, *C*). The upper part of the embryo develops upward, organizing the seta and capsule. In true Mosses, when the embryo becomes too large for the venter of the archegonium in which it is developing, the archegonium is broken near the base of the venter and is carried upward perched on the top

of the capsule like a loose cap or hood, known as the *calyptra* (Figs. 82, *c*, 107), which sooner or later falls off. As stated before, the mature structure developed from the oospore is called a sporogonium, a form of sporophyte peculiar to the Bryophytes.

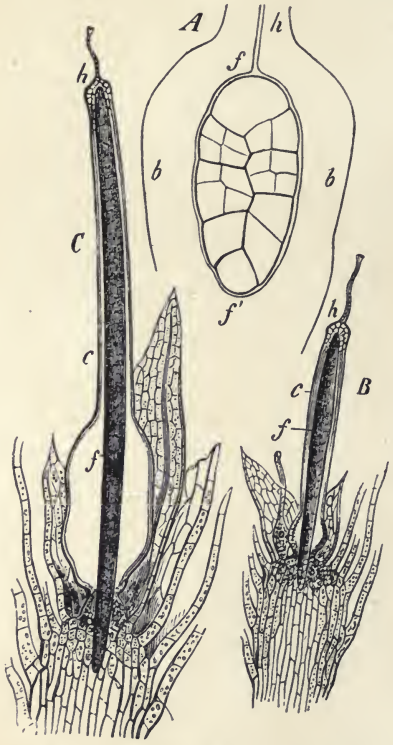


FIG. 85. Sporogonium of *Funaria*: *A*, an embryo sporogonium (*f*, *f'*), developing within the venter (*b*, *b*) of an archegonium; *B*, *C*, tips of leafy shoots bearing young sporogonia, pushing up calyptra (*c*) and archegonium neck (*h*), and sending the foot down into the apex of the gametophore.—After GOEBEL.

66. **The sporogonium.** —In its fullest development the sporogonium is differentiated into the three regions, foot, seta, and capsule (Figs. 82, 107); but in some forms the seta may be lacking, and in others the foot also, the sporogonium in this last case being only the capsule or spore case, which, after all, is the essential part of any sporogonium.

At first the capsule is solid, and its cells are all alike. Later a group of cells within begins to differ in appearance from those about them, being set apart for the production of spores. This initial group of spore-producing cells is called the *archesporium*, a word meaning "the beginning of spores." It

does not follow that the archesporial cells themselves produce spores, but that the spores are to appear sooner or later in their progeny. Usually the archesporial cells divide and form a larger mass of spore-producing cells. Such cells are known as *sporogenous* ("spore-producing") *cells,* or the group is spoken of as *sporogenous tissue.* Sporogenous cells may divide more or less, and the cells of the last division are mother cells, those which directly produce the spores. The usual sequence, therefore, is archesporial cells (archesporium), sporogenous cells, and mother cells; but it must be remembered that they all may be referred to as sporogenous cells.

Each mother cell organizes within itself four spores, the group being known as a *tetrad.* In Bryophytes and the higher groups asexual spores are always produced in tetrads. After the spores are formed the walls of the mother cells disorganize, and the spores are left lying loose in a cavity which was formerly occupied by the sporogenous tissue. All mother cells do not always organize spores. In some cases some of them are used up in supplying nourishment to those which form spores. Such mother cells are said to function as nutritive cells. In other cases, certain mother cells become much modified in form, being organized into elongated, spirally-banded cells called *elaters* (Figs. 97, 101), meaning "drivers" or "hurlers." These elaters lie among the loose ripe spores, are discharged with them, and by their jerking movements assist in scattering them.

The cells of the sporogonium which do not enter into the formation of the archesporium, and are not sporogenous, are said to be *sterile,* and are often spoken of as *sterile tissue.* Every sporogonium, therefore, is made up of sporogenous tissue and sterile tissue, and the differences found among the sporogonia of Bryophytes depend upon the relative display of these two tissues.

The sporogonium is a very important structure from the standpoint of evolution, for it represents the conspicu-

ous part of the higher plants. The "fern plant," and the herbs, shrubs, and trees among "flowering plants" correspond to the sporogonium of Bryophytes, and not to the leafy branch (gametophore) or "moss plant." Consequently the evolution of the sporogonium through the Bryophytes is traced with a great deal of interest. It may be outlined as follows:

In a liverwort called *Riccia* the simplest sporogonium is found. It is a globular capsule, without seta or foot

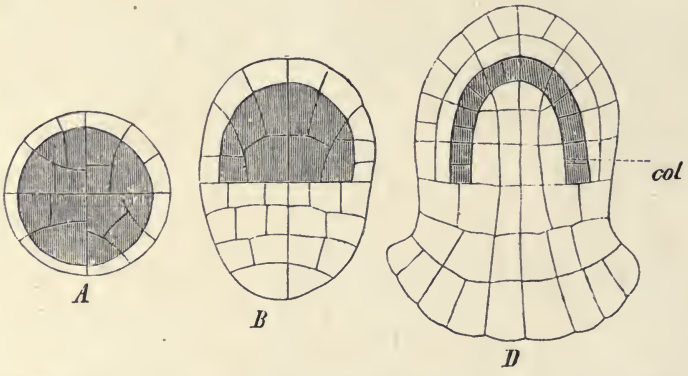


FIG. 86. Diagrammatic sections of sporogonia of liverworts: *A*, *Riccia*, the whole capsule being archesporium except the sterile wall layer; *B*, *Marchantia*, one half the capsule being sterile, the archesporium restricted to the other half; *D*, *Anthoceros*, archesporium still more restricted, being dome-shaped and capping a central sterile tissue, the columella (*col*).—After GOEBEL.

(Fig. 86, *A*). The only sterile tissue is the single layer of cells forming the wall, all the cells within the wall belonging to the archesporium. The ripe sporogonium, therefore, is nothing but a thin-walled spore case. It is well to note that the sporophyte thus begins as a spore case, and that any additional structures that it may develop later are secondary.

In another liverwort (*Marchantia*) the entire lower half of the sporogonium is sterile, while in the upper half there

is a single layer of sterile cells as a wall about the archesporium, which is composed of all the remaining cells of the upper half (Fig. 86, *B*). It will be noted that the sterile tissue in this sporogonium has encroached upon the archesporium, which is restricted to one half of the body. In this case the archesporium has the form of a hemisphere.

In another liverwort (*Jungermannia*) the archesporium is still more restricted (Fig. 87). The sterile tissue is organized into a foot and a seta, and the archesporium is a comparatively small mass of cells in the upper part of the sporogonium.

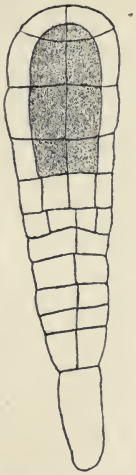


FIG. 87. Diagrammatic section of sporogonium of a *Jungermannia* form, showing differentiation into foot, seta, and capsule, the archesporium restricted to upper part of sporogonium.—After GOEBEL.

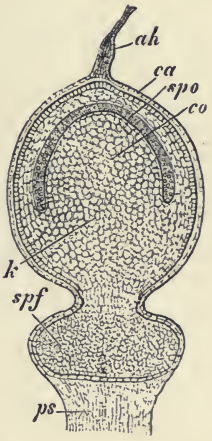


FIG. 88. Section through sporogonium of *Sphagnum*, showing capsule (*k*) with old archegonium neck (*ah*), calyptra (*ca*), dome-shaped mass of sporogenous tissue (*spo*), and columella (*co*), also the bulbous foot (*spf*) imbedded in the pseudopodium (*ps*).—After SCHIMPER.

In another liverwort (*Anthoceros*) the sterile tissue organizes foot and seta, and the archesporium is still more restricted (Fig. 86, *D*). Instead of a solid hemispherical

mass, it is a dome-shaped mass, the inner cells of the hemisphere having become sterile. This central group of sterile cells which is surrounded by the archesporium is called the *columella*, which means "a small column."

Fig. 89. Young sporogonium of a true moss, showing foot, seta, and young capsule, in which the archesporium (darker portion) is barrel-shaped, and through it the columella is continuous with the lid.—After Campbell.

In a moss called *Sphagnum* there is the same dome-shaped archesporium with the columella, as in *Anthoceros*, but it is relatively smaller on account of the more abundant sterile tissue (Fig. 88).

In the highest Mosses the archesporium becomes very small as compared with the sterile tissue (Fig. 89). A foot, a long seta, and an elaborate capsule are organized from the sterile tissue, while the archesporium is shaped like the walls of a barrel, as though the dome-shaped archesporium of *Sphagnum* or *Anthoceros* had become sterile at the apex. In this way the columella is continued through the capsule, and is not capped by the archesporium.

This series indicates that after the sporogonium begins as a simple spore case (*Riccia*), its tendency is to increase sterile tissue and to restrict sporogenous tissue, using the sterile tissue in the formation of the organs of the sporogonium body, as foot, seta, capsule walls, etc.

Among the Green Algæ there is a form known as *Coleochæte*, whose body resembles those of the simplest Liverworts (Fig. 90). When

its oospores germinate there is formed a globular mass of cells, every one of which is a spore mother cell (Fig. 90, *C*). If an outer layer of mother cells should become sterile and form a wall about the others, such a spore case as that of

FIG. 90.—*Coleochæte*, one of the green algæ: *A*, a portion of the thallus, showing oogonia with trichogynes (*og*), antheridia (*an*), and two enlarged biciliate sperms (*z*); *B*, a fertilized oogonium containing oospore and invested by a tissue (*r*) which has developed after fertilization; *C*, an oospore which has germinated and formed a mass of cells (probably a sporophyte), each one of which organizes a biciliate zoospore (*D*).—After PRINGSHEIM.

Riccia would be the result (Fig. 86, *A*). For such reasons many believe that the Liverworts have been derived from such forms as *Coleochæte*.

67. **The gametophyte.**—Having considered the sporophyte body as represented by the sporogonium, we must consider the gametophyte body as represented by protonema and leafy branch (gametophore). The gametophyte results from the germination of an asexual spore, and in the Mosses it is differentiated into protonema and leafy gametophore (Figs. 81, 82, 102). Like the sporophyte,

however, it shows an interesting evolution from its simplest condition in the Liverworts to its most complex condition in the true Mosses.

In the Liverworts the spore develops a flat thallus body, one plate of cells or more in thickness, which generally branches dichotomously (see § 29) and forms a more or less extensive body (Fig. 92). This thallus is the gametophyte, there being no differentiation into protonema and leafy branch.

In the simpler Liverworts the sex organs (antheridia and archegonia) are scattered over the back of this thallus (Fig. 92). In other forms they become collected in certain definite regions of the thallus. In other forms these definite sexual regions become differentiated from the rest of the thallus as disks. In other forms these disks, bearing the sex organs, become short-stalked, and in others long-stalked, until a regular branch arises from the thallus body (Figs. 96, 97). This erect branch, bearing the sex organs, is, of course, a gametophore, but it is leafless, the thallus body doing the chlorophyll work.

In the *Sphagnum* Mosses the spore develops the same kind of flat thallus (Fig. 104), but the gametophore becomes leafy, sharing the chlorophyll work with the thallus. In the true Mosses most of the chlorophyll work is done by the leafy gametophore, and the flat thallus is reduced to branching filaments (the protonema) (Fig. 102).

The protonema of the true Mosses, therefore, corresponds to the flat thallus of the Liverworts and *Sphagnum*, while the leafy branch corresponds to the leafless gametophore found in some Liverworts. It also seems evident that the gametophore was originally set apart to bear sex organs, and that the leaves which appear upon it in the Mosses are subsequent structures.

CHAPTER VIII

THE GREAT GROUPS OF BRYOPHYTES

Hepaticæ (*Liverworts*)

68. **General character.**—Liverworts live in a variety of conditions, some floating on the water, many in damp places, and many on the bark of trees. In general they are moisture-loving plants (hydrophytes), though some can endure great dryness. The gametophyte body is prostrate, though there may be erect and leafless gametophores.

This prostrate habit develops a *dorsiventral* body—that is, one whose two surfaces (*dorsal* and *ventral*) are exposed to different conditions and become unlike in structure. In Liverworts the ventral surface is against the substratum, and puts out numerous hair-like processes (*rhizoids*) for absorption and anchorage. The dorsal region is exposed to the light and its cells develop chlorophyll. If the thallus is thin, chlorophyll is developed in all the cells; if it be so thick that the light is cut off from the ventral cells, the thallus is differentiated into a green dorsal region doing the chlorophyll work, and a colorless ventral region producing absorbing rhizoids. This latter represents a simple differentiation of the nutritive body into working regions, the ventral region absorbing material and conducting it to the green dorsal cells which use it in making food.

There seems to have been at least three main lines of development among Liverworts, each beginning in forms with a very simple thallus, and developing in different directions. They are briefly indicated as follows:

69. **Marchantia forms.**—In this line the simple thallus gradually becomes changed into a very complex one. The thallus retains its simple outlines, but becomes thick and differentiated in *tissues* (groups of similar cells). The line may be distinguished, therefore, as one in which the differentiation of the tissues of the gametophyte is emphasized (Figs. 91–93). In *Marchantia* proper the thallus becomes very complex, and it may be taken as an illustration.

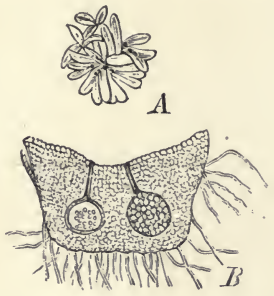


FIG. 91. A very small species of *Riccia*, one of the Marchantia forms: *A*, a group of thallus bodies slightly enlarged; *B*, section of a thallus, showing rhizoids and two sporogonia imbedded and communicating with the outside by tubular passages in the thallus.—After STRASBURGER.

The thallus is so thick that there are very distinct green dorsal and colorless ventral regions (Fig. 94). The latter puts out numerous rhizoids and scales from the single layer of epidermal cells. Above the ventral epidermis are several layers of colorless

FIG. 92. *Ricciocarpus*, a Marchantia form, showing numerous rhizoids from ventral surface, the dichotomous branching, and the position of the sporogonia on the dorsal surface along the "midribs."—CALDWELL.

Fig. 93. Two common liverworts: to the left is *Conocephalus*, a Marchantia form, showing rhizoids, dichotomous branching, and the conspicuous rhombic areas (areolæ) on the dorsal surface; to the right is *Anthoceros*, with its simple thallus and pod-like sporogonia.—Caldwell.

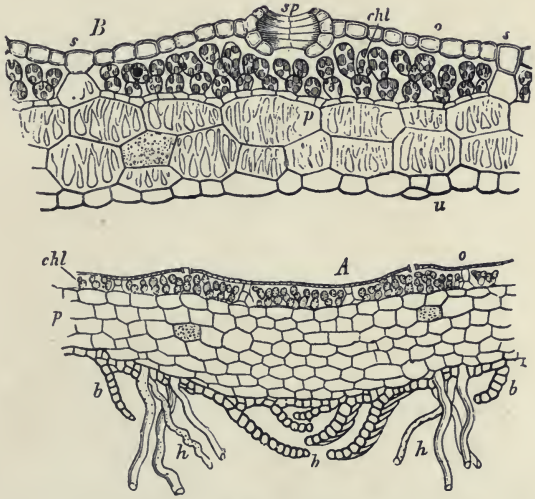


Fig. 94. Cross-sections of thallus of *Marchantia*: *A*, section from thicker part of thallus, where supporting tissue (*p*) is abundant, and showing lower epidermis giving rise to rhizoids (*h*) and plates (*b*), also chlorophyll tissue (*chl*) organized into chambers by partitions (*o*); *B*, section near margin of thallus more magnified, showing lower epidermis, two layers of supporting tissue (*p*) with reticulate walls, a single chlorophyll chamber with its bounding walls (*s*) and containing short, often branching filaments whose cells contain chloroplasts (*chl*), overarching upper epidermis (*o*) pierced by a large chimney-like air-pore (*sp*).—After Goebel.

FIG. 95. Section through cupule of *Marchantia*, showing wall in which are chlorophyll-bearing air-chambers with air-pores, and gemmæ (*a*) in various stages of development.—After KNY.

FIG. 96. *Marchantia polymorpha*: the lower figure represents a gametophyte bearing a mature antheridial branch (*d*), some young antheridial branches, and also some cupules with toothed margins, in which the gemmæ may be seen; the upper figure represents a partial section through the antheridial disk, and shows antheridia within the antheridial cavities (*a, b, c, d, e, f*).—After KNY.

cells more or less modified for conduction. Above these the dorsal region is organized into a series of large air chambers, into which project chlorophyll-containing cells in the

FIG. 97. *Marchantia polymorpha*, a common liverwort: *1*, thallus, with rhizoids, bearing a mature archegonial branch (*f*) and several younger ones (*a*, *b*, *c*, *d*, *e*); *2* and *3*, dorsal and ventral views of archegonial disk; *4* and *5*, young sporophyte (sporogonium) embryos; *6*, more mature sporogonium still within enlarged venter of archegonium; *7*, mature sporogonium discharging spores; *8*, three spores and an elater.—After KNY.

form of short branching filaments. Overarching the air chambers is the dorsal epidermis, and piercing through it into each air chamber is a conspicuous air pore (Fig. 94, *B*).

The air chambers are outlined on the surface as small rhombic areas (*areolæ*), each containing a single air pore.

Peculiar reproductive bodies are also developed upon the dorsal surface of *Marchantia* for vegetative multiplica-

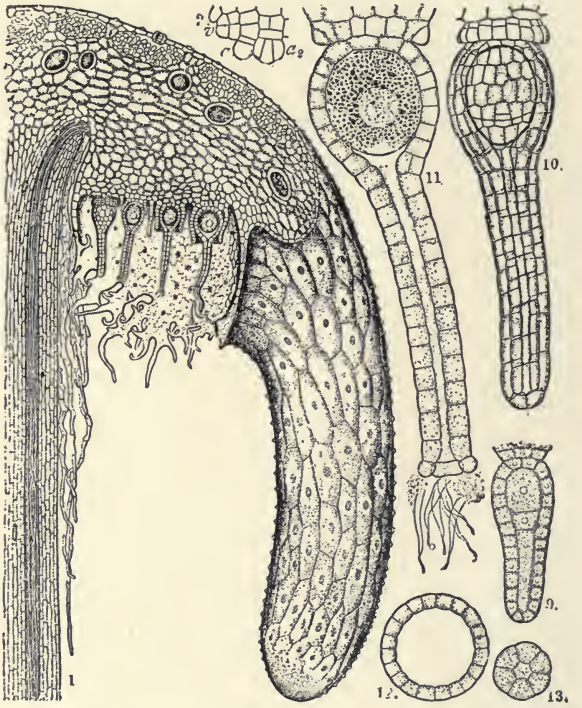


Fig. 98. *Marchantia polymorpha*: *1*, partial section through archegonial disk, showing archegonia with long necks, and venters containing eggs; *9*, young archegonium showing axial row; *10*, superficial view at later stage; *11*, mature archegonium, with axial row disorganized and leaving an open passage to the large egg; *12*, cross-section of venter; *13*, cross-section of neck.—After Kny.

tion. Little cups (*cupules*) appear, and in them are numerous short-stalked bodies (*gemmæ*), which are round and flat (biscuit-shaped) and many-celled (Figs. 95, 96). The

gemmæ fall off and develop new thallus bodies, making rapid multiplication possible.

Marchantia also possess remarkably prominent gametophores, or "sexual branches" as they are often called. In this case the gametophores are differentiated, one bearing only antheridia (Fig. 96), and known as the "antheridial branch," the other bearing only archegonia (Figs. 97, 98), and known as the "archegonial branch." The scalloped antheridial disk and the star-shaped archegonial disk, each borne up by the stalk-like gametophore, are seen in the illustrations. Not only are the gametophores sexually differentiated, but as only one appears on each thallus, the thallus bodies are sexually differentiated. When the two sex organs appear upon different individuals, the plant is said to be *diœcious*, meaning "two households"; when they both appear upon the same individual, the plant is *monœcious*, meaning "one household." Some of the Bryophytes are monœcious, and some of them are diœcious (as *Marchantia*).

Another distinguishing mark of the line of *Marchantia* forms is that the capsule-like sporogonium opens irregularly to discharge its spores (Fig. 97, 7).

70. **Jungermannia forms.**—This is the greatest line of the Liverworts, the forms being much more numerous than in the other lines. They grow in damp places; or in drier situations on rocks, ground, or tree-trunks; or in the tropics also on the leaves of forest plants. They are generally delicate plants, and resemble small Mosses, many of them doubtless being commonly mistaken for Mosses.

This resemblance to Mosses suggests one of the chief features of the line. Beginning with a simple thallus, as in the *Marchantia* line, the structure of the thallus remains simple, there being no such differentiation of tissues as in the *Marchantia* line; but the form of the thallus becomes much modified (Figs. 99, 100). Instead of a flat thallus with even outline, the body is organized into a central stem-like axis bearing two rows of small, often crowded

leaves. There are really three rows of leaves, but the third is on the ventral side against the substratum, and is often so much modified as not to look like the other leaves. In consequence of this the *Jungermannia* forms are usually called "leafy liverworts," to distinguish them from the

FIG. 99. Two liverworts, both Jungermannia forms: to the left is *Blasia*, which retains the thallus form but has lobed margins; to the right is *Scapania*, with distinct leaves and sporogonia (*A*).—CALDWELL.

other Liverworts, which are "thallose." They are also often called "scale mosses," on account of their moss-like appearance and their small scale-like leaves.

The line may be distinguished, therefore, as one in which the differentiation of the form of the gametophyte is emphasized. Another distinguishing mark is that the sporogonium has a prominent seta, and the capsule splits down into four pieces (*valves*) when opening to discharge the spores (Fig. 100, *C*).

71. **Anthoceros forms.**—This line contains comparatively few forms, but they are of great interest, as they are supposed to represent forms which have given rise to the

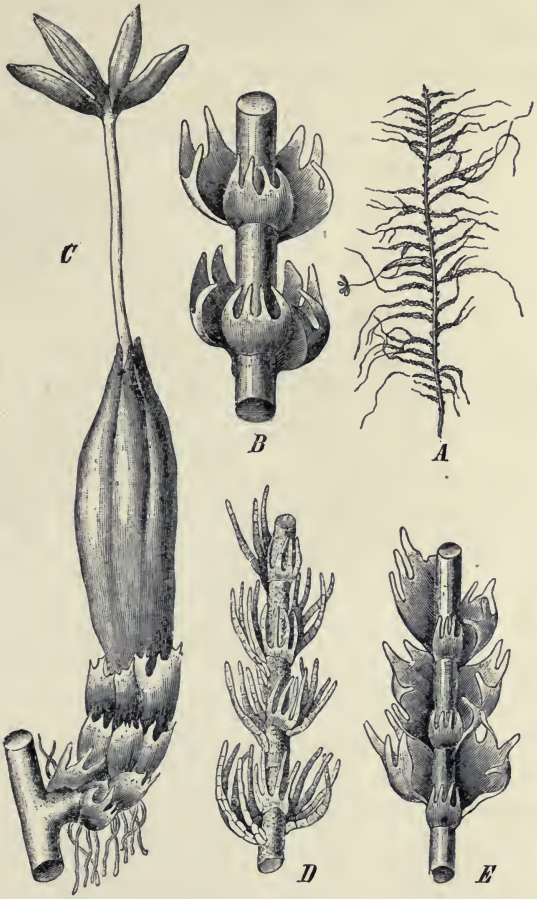


FIG. 100. Species of *Lepidozia*, a genus of leafy liverworts, showing different leaf forms, and in *A* and *C* the dehiscence of the sporogonium by four valves. In *C* rhizoids are evident; and in *B*, *D*, and *E* the three rows of leaves are seen, the leaves of the ventral row being comparatively small.—After ENGLER and PRANTL.

Mosses, and possibly to the Pteridophytes also. The thallus is very simple, being differentiated neither in structure nor form, as in the two other lines; but the

special development has been in connection with the sporogonium (Figs. 93, 101).

This complex sporogonium (sporophyte) has a large bulbous foot imbedded in the simple thallus, while above there arises a long pod-like capsule. The complex walls of this capsule contain chlorophyll and air pores, so that the sporogonium is organized for chlorophyll work. If the foot could send absorbing processes into the soil, this sporophyte could live independent of the gametophyte. In opening to discharge spores the pod-like capsule splits down into two valves.

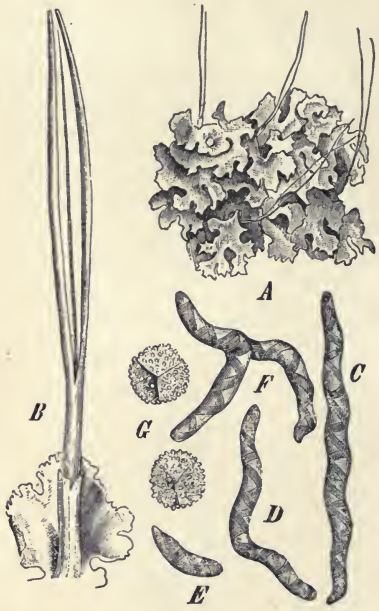


FIG. 101. *Anthoceros gracilis*: *A*, several gametophytes, on which sporogonia have developed; *B*, an enlarged sporogonium, showing its elongated character and dehiscence by two valves leaving exposed the slender columella on the surface of which are the spores; *C*, *D*, *E*, *F*, elaters of various forms; *G*, spores.—After SCHIFFNER.

Another peculiarity of the *Anthoceros* forms is in connection with the antheridia and archegonia. These organs, instead of growing out free from the body of the thallus, as in other Liverworts, are imbedded in it. The significance of this peculiarity lies in the fact that it is a character which belongs to the Pteridophytes.

The chief direction of development of the three liverwort lines may be summed up briefly as follows: The *Marchantia* line has differentiated the structure of the

gametophyte; the *Jungermannia* line has differentiated the form of the gametophyte; the *Anthoceros* line has differentiated the structure of the sporophyte. It should be remembered that other characters also serve to distinguish the lines from one another.

Musci (*Mosses*)

72. **General character.**—Mosses are highly specialized plants, probably derived from Liverworts, the numerous forms being adapted to all conditions, from submerged to very dry, being most abundantly displayed in temperate and arctic regions. Many of them may be dried out completely and then revived in the presence of moisture, as is true of many Lichens and Liverworts, with which forms Mosses are very commonly associated.

They also have great power of vegetative multiplication, new leafy shoots putting out from old ones and from the protonema indefinitely, thus forming thick carpets and masses. Bog mosses often completely fill up bogs or small ponds and lakes with a dense growth, which dies below and continues to grow above as long as the conditions are favorable. These quaking bogs or "mosses," as they are sometimes called, furnish very treacherous footing unless rendered firmer by other plants. In these moss-filled bogs the water and silt shut off the lower strata of moss from complete disorganization, and they become modified into a coaly substance called *peat*, which may accumulate to considerable thickness by the continued upward growth of the mass of moss.

The gametophyte body is differentiated into two very distinct regions: (1) the prostrate dorsiventral thallus, which is called protonema in this group, and which may be either a broad flat thallus (Fig. 104) or a set of branching filaments (Figs. 81, 102); (2) the erect leafy branch or gametophore (Fig. 82). This erect branch is said to be

radial, in contrast with the dorsiventral thallus, referring to the fact that it is exposed to similar conditions all around, and its organs are arranged about a central axis like the parts of a radiate animal. This position is much more favorable for the chlorophyll work than the dorsiventral position, as the special chlorophyll organs (leaves) can be spread out to the light freely in all directions.

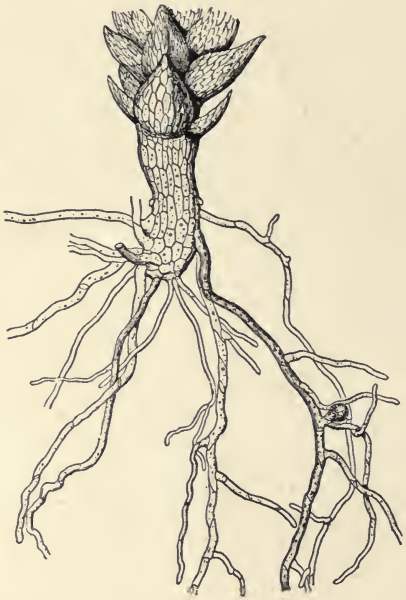


FIG. 102. A moss (*Bryum*), showing base of a leafy branch (gametophore) attached to the protonema, and having sent out rhizoids. On the protonemal filament to the right and below is the young bud of another leafy branch. —MÜLLER.

It should be remarked that the gametophyte in all groups of plants is a thallus, doing its chlorophyll work, when it does any, in a dorsiventral position; the only exception being the radial leafy branch that arises from the thallus of Mosses. From Mosses onward the gametophyte becomes less conspicuous, so that the prominent leafy plants of the higher groups hold no relation to the little erect leafy branch of the Mosses, which is put out by the gametophyte, and which is the best the gametophyte ever does toward getting into a better position for chlorophyll work.

The leafy branch of the Mosses usually becomes independent of the thallus by putting out rhizoids at its base

(Fig. 102), the thallus part dying. Sometimes, however, the filamentous protonema is very persistent, and gives rise to a perennial succession of leafy branches.

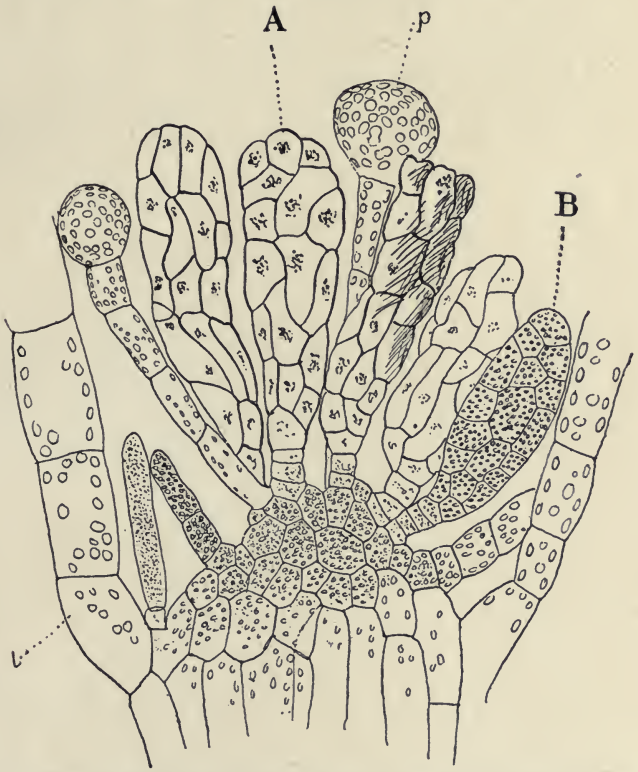


FIG. 103. Tip of leafy branch of a moss (*Funaria*), bearing a cluster of sex organs, showing an old antheridium (*A*), a younger one (*B*), some of the curious associated hairs (*p*), and leaf sections (*l*).—After CAMPBELL.

At the summit of the leafy gametophore, either upon the main axis or upon a lateral branch, the antheridia and archegonia are borne (Figs. 83, 103). Often the leaves at the summit become modified in form and arranged to form

a rosette, in the center of which are the sex organs. This rosette is often called the "moss flower," but it holds no relation to the flower of Seed-plants, and the phrase should not be used. A rosette may contain but one kind of sex organ (Figs. 83, 103), or it may contain both kinds, for Mosses are both dicœcious and monœcious. The two principal groups are as follows :

73. **Sphagnum forms.**—These are large and pallid bog mosses, found abundantly in marshy ground, especially of temperate and arctic regions, and are conspicuous peat-formers (Fig. 105, *A*). The leaves and gametophore axis are of peculiar structure to enable them to suck up and hold a large amount of water. This abundant water-storage tissue and the comparatively poor display of chlorophyll-containing cells gives the peculiar pallid appearance.

FIG. 104. Thallus body of gametophyte of *Sphagnum*, giving rise to rhizoids (*r*) and buds (*k*) which develop into the large leafy branches (gametophores).—After CAMPBELL.

They resemble the Liverworts in the broad thallus body of the gametophyte, from which the large leafy gametophore arises (Fig. 104). They also resemble *Anthoceros* forms in the sporogonium, the archesporium being a dome-shaped mass (Fig. 105, *C*). On the other hand, they resemble the true Mosses, not only in the leafy gametophore, but also in the fact that the capsule opens at the apex by a circular lid, called the *operculum* (Fig.

105, *D*), which means a "cover" or "lid." This may serve to illustrate what is called an "intermediate" or "transition" type, *Sphagnum* showing characters which ally it to *Anthoceros* forms on the one side, and to true Mosses on the other.

A peculiar feature of the sporogonium is that it has no long stalk-like seta, as have the true Mosses, although it appears to have one. This false appearance arises from the

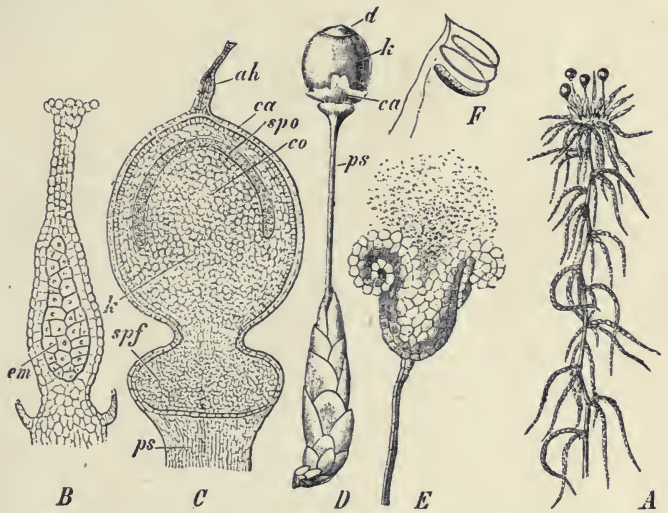


FIG. 105. *Sphagnum*: *A*, a leafy branch (gametophore) bearing four mature sporogonia; *B*, archegonium in whose venter a young embryo sporophyte (*em*) is developing; *C*, section of a young sporogonium (sporophyte), showing the bulbous foot (*spf*) imbedded in the apex of the pseudopodium (*ps*), the capsule (*k*), the columella (*co*) capped by the dome-shaped archesporium (*spo*), a portion of the calyptra (*ca*), and the old archegonium neck (*ah*); *D*, branch bearing mature sporogonium and showing pseudopodium (*ps*), capsule (*k*), and operculum (*d*); *E*, antheridium discharging sperms; *F*, a single sperm, showing coiled body and two cilia.—After SCHIMPER.

fact that the axis of the gametophore is prolonged above its leafy portion, the prolongation resembling the seta of an ordinary moss (Fig. 105, *D*). This prolongation is

called a *pseudopodium*, or "false stalk," and in the top of it is imbedded the foot of the sporogonium carrying the globular capsule (Fig. 105, *C*).

74. **True Mosses.**—This immense and most highly organized Bryophyte group contains the great majority of the Mosses, which are sometimes called the *Bryum* forms, to distinguish them from the *Sphagnum* forms. They are

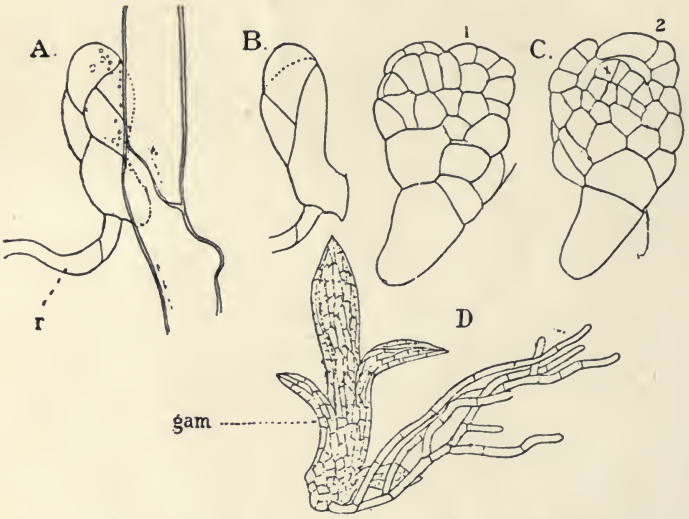


Fig. 106. Different stages in the development of the leafy gametophore from the protonema of a common moss (*Funaria*): *A*, the first few cells and a rhizoid (*r*); *B*, *C*, later stages, showing apical cell (*1*) and young leaves (*2*); *D*, later stage much less magnified, showing protonemal filaments and the young gametophore (*gam*) —After Campbell.

the representative Bryophytes, the only group vying with them being the leafy Liverworts, or *Jungermannia* forms. They grow in all conditions of moisture, from actual submergence in water to dry rocks, and they also form extensive peat deposits in bogs.

The thallus body of the gametophyte is made up of branching filaments (Figs. 81, 102), those exposed to the

light containing chlorophyll, and those in the substratum being colorless and acting as rhizoids. The leafy gametophores are often highly organized (Figs. 102, 106), the leaves and stems showing a certain amount of differentiation of tissues.

It is the sporophyte, however, which shows the greatest amount of specialization (Fig. 107). The sporogonium

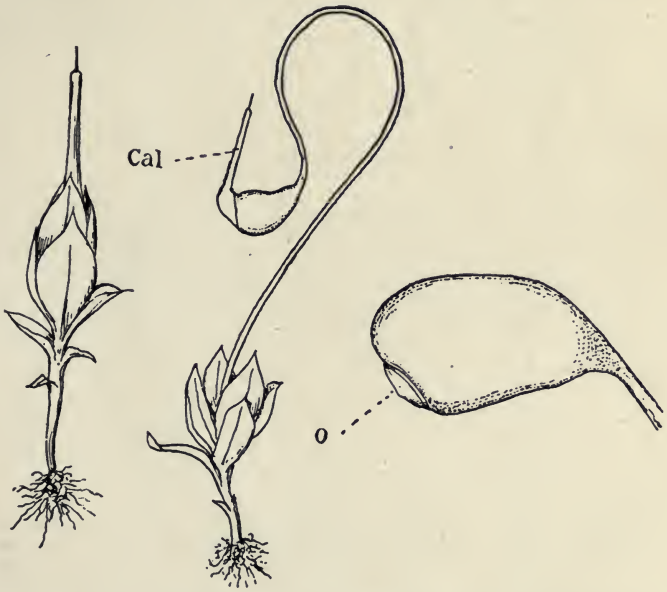


Fig. 107. A common moss (*Funaria*): in the center is the leafy shoot (gametophore), with rhizoids, several leaves, and a sporogonium (sporophyte), with a long seta, capsule, and at its tip the calyptra (*cal*); to the right a capsule with calyptra removed, showing the operculum (*o*); to the left a young sporogonium pushing up the calyptra from the leafy shoot.—After Campbell.

has a foot and a long slender seta, but the capsule is especially complex. The archesporium is reduced to a small hollow cylinder (Fig. 88), the capsule wall is most elaborately constructed, and the columella runs through the

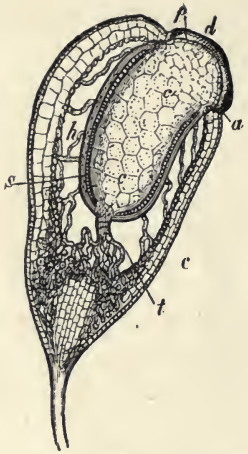


FIG. 108. Longitudinal section of moss capsule (*Funaria*), showing its complex character: *d*, operculum; *p*, peristome: *c*, *c'*, columella; *s*, sporogenous tissue; outside of *s* the complex wall consisting of layers of cells and large open spaces (*h*) traversed by strands of tissue.—After GOEBEL.

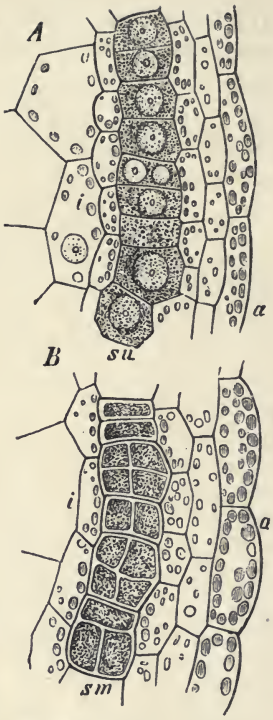


FIG. 109. Partial longitudinal section through a moss capsule: *A*, younger capsule, showing wall cells (*a*), cells of columella (*i*), and sporogenous cells (*su*); *B*, somewhat older capsule, *a* and *i* same as before, and *sm* the spore mother cells. — After GOEBEL.

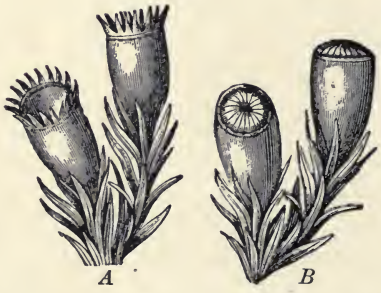


FIG. 110. Sporogonia of *Grimmia*, from all of which the operculum has fallen, displaying the peristome teeth: *A*, position of the teeth when dry; *B*, position when moist.—After KERNER.

center of the capsule to the lid-like operculum (Figs. 108, 109). When the operculum falls off the capsule is left like an urn full of spores, and at the mouth of the urn there is usually displayed a set of slender, often very beautiful teeth (Fig. 110), radiating from the circumference to the center, and called the *peristome*, meaning "about the mouth." These teeth are hygroscopic, and by bending inward and outward help to discharge the spores.

CHAPTER IX

PTERIDOPHYTES (FERN PLANTS)

75. **Summary from Bryophytes.**—In introducing the Bryophytes a summary from the Thallophytes was given (see § 60), indicating certain important things which that group has contributed to the evolution of the plant kingdom. In introducing the Pteridophytes it is well to notice certain important additions made by the Bryophytes.

(1) *Alternation of generations.*—The great fact of alternating sexual (gametophyte) and sexless (sporophyte) generations is first clearly expressed by the Bryophytes, although its beginnings are to be found among the Thallophytes. Each generation produces one kind of spore, from which is developed the other generation.

(2) *Gametophyte the chlorophyll generation.*—On account of this fact the food is chiefly manufactured by the gametophyte, which is therefore the more conspicuous generation. When a moss or a liverwort is spoken of, therefore, the gametophyte is usually referred to.

(3) *Gametophyte and sporophyte not independent.*—The sporophyte is mainly dependent upon the gametophyte for its nutrition, and remains attached to it, being commonly called the sporogonium, and its only function is to produce spores.

(4) *Differentiation of thallus into stem and leaves.*—This appears incompletely in the leafy Liverworts (*Jungermannia* forms) and much more clearly in the erect and radial leafy branch (gametophore) of the Mosses.

(5) *Many-celled sex organs.*—The antheridia and the flask-shaped archegonia are very characteristic of Bryophytes as contrasted with Thallophytes.

76. **General characters of Pteridophytes.**—The name means "fern plants," and the Ferns are the most numerous and the most representative forms of the group. Associated with them, however, are the Horsetails (Scouring rushes) and the Club-mosses. By many the Pteridophytes are thought to have been derived from such Liverworts as the *Anthoceros* forms, while some think that they may possibly have been derived directly from the Green Algæ. Whatever their origin, they are very distinct from Bryophytes.

One of the very important facts is the appearance of the vascular system, which means a "system of vessels," organized for conducting material through the plant body. The appearance of this system marks some such epoch in the evolution of plants as is marked in animals by the appearance of the "backbone." As animals are often grouped as "vertebrates" and "invertebrates," plants are often grouped as "vascular plants" and "non-vascular plants," the former being the Pteridophytes and Spermatophytes, the latter being the Thallophytes and Bryophytes. Pteridophytes are of great interest, therefore, as being the first vascular plants.

77. **Alternation of generations.**—This alternation continues in the Pteridophytes, but is even more distinct than in the Bryophytes, the gametophyte and sporophyte becoming independent of one another. An outline of the life history of an ordinary fern will illustrate this fact, and will serve also to point out the prominent structures. Upon the lower surface of the leaves of an ordinary fern dark spots or lines are often seen. These are found to yield spores, with which the life history may be begun.

When such a spore germinates it gives rise to a small, green, heart-shaped thallus, resembling a delicate and simple liverwort (Fig. 111, *A*). Upon this thallus antheridia

and archegonia appear, so that it is evidently a gametophyte. This gametophyte escapes ordinary attention, as it is usually very small, and lies prostrate upon the substratum. It has received the name *prothallium* or *prothallus*, so that when the term prothallium is used the gametophyte of Pteridophytes is generally referred to; just as when the term sporogonium is used the sporophyte of the Bryophytes is referred to. Within an archegonium borne upon this little prothallium an oospore is formed. When the oospore ger-

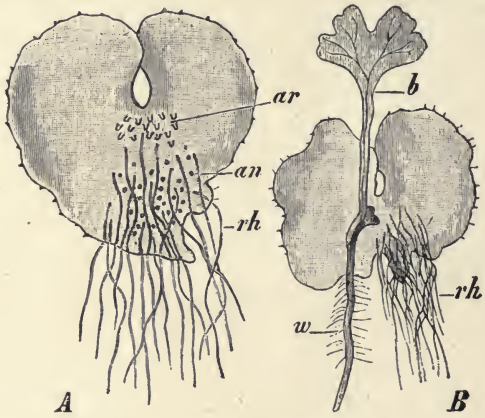


FIG. 111. Prothallium of a common fern (*Aspidium*): *A*, ventral surface, showing rhizoids (*rh*), antheridia (*an*), and archegonia (*ar*); *B*, ventral surface of an older gametophyte, showing rhizoids (*rh*) and young sporophyte with root (*w*) and leaf (*b*).—After SCHENCK.

minates it develops the large leafy plant ordinarily spoken of as "the fern," with its subterranean stem, from which roots descend, and from which large branching leaves rise above the surface of the ground (Fig. 111, *B*). It is in this complex body that the vascular system appears. No sex organs are developed upon it, but the leaves bear numerous sporangia full of asexual spores. This complex vascular plant, therefore, is a sporophyte, and corresponds in this life history to the sporogonium of the Bryophytes. This

completes the life cycle, as the asexual spores develop the prothallium again.

In contrasting this life history with that of Bryophytes several important differences are discovered. The most striking one is that the sporophyte has become a large, leafy, vascular, and independent structure, not at all resembling its representative (the sporogonium) among the Bryophytes.

Also the gametophyte has become much reduced, as compared with the gametophytes of the larger Liverworts and Mosses. It seems to have resumed the simplest liverwort form, even the gametophore being suppressed, and represented, if at all, by a rudiment. The conspicuous leafy branch of the Mosses, commonly called "the moss plant," corresponds to nothing in the Pteridophytes, therefore, except possibly the rudiment referred to, the prothallium representing only the protonema part of the gametophyte of the true Mosses.

This reduction of the gametophyte seems to be associated with the fact that the chlorophyll work has been transferred to the sporophyte, which hereafter remains the conspicuous generation. The "fern plant" of ordinary observation, therefore, is the sporophyte; while the "moss plant" is a leafy branch of the gametophyte.

Another important contrast indicated is that in Bryophytes the sporophyte is dependent upon the gametophyte for its nutrition, remaining attached to it; while in the Pteridophytes both generations are independent green plants, the leafy sporophyte remaining attached to the small gametophyte only while beginning its growth (Fig. 111, *B*).

Among the Ferns some interesting exceptions to this method of alternation have been observed. Under certain conditions a leafy sporophyte may sprout directly from the prothallium (gametophyte) instead of from an oospore. This is called *apogamy*, meaning "without the sexual act."

Under certain other conditions prothallia are observed to sprout directly from the leafy sporophyte instead of from a spore. This is called *apospory,* meaning "without a spore."

78. **The gametophyte.**—The prothallium, like a simple liverwort, is a dorsiventral body, and puts out numerous

FIG. 112. Stag-horn fern (*Platycerium grande*), an epiphytic tropical form, showing the two forms of leaves: *a* and *b*, young sterile leaves; *c*, leaves bearing sporangia; *d*, an old sterile leaf.—CALDWELL.

rhizoids from its ventral surface (Fig. 111). It is so thin that all the cells contain chlorophyll, and it is usually short-lived. In rare cases it becomes quite large and permanent,

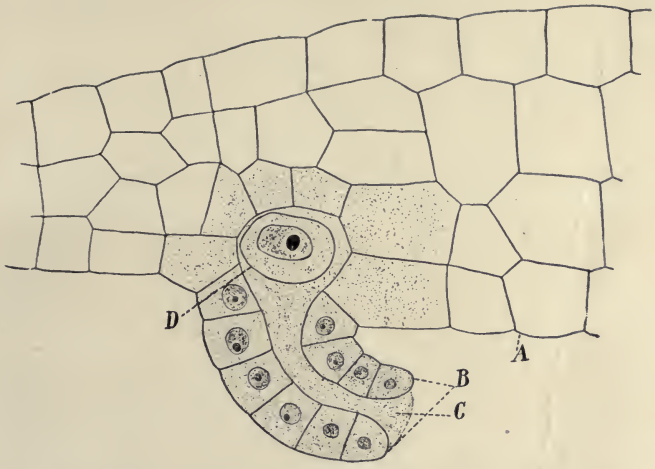


FIG. 113. Archegonium of *Pteris* at the time of fertilization, showing tissue of gametophyte (*A*), the cells forming the neck (*B*), the passageway formed by the disorganization of the canal cells (*C*), and the egg (*D*) lying exposed in the venter. —CALDWELL.

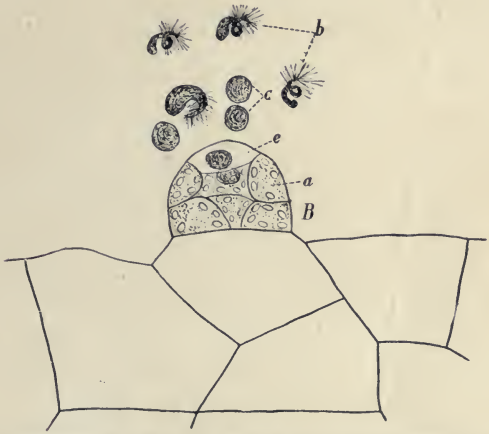


FIG. 114. Antheridium of *Pteris* (*B*), showing wall cells (*a*), opening for escape of sperm mother cells (*e*), escaped mother cells (*c*), sperms free from mother cells (*b*), showing spiral and multiciliate character.—CALDWELL.

being a conspicuous object in connection with the sporophyte.

At the bottom of the conspicuous notch in the prothallium is the growing point, representing the apex of the plant. This notch is always a conspicuous feature.

The antheridia and archegonia are usually developed on the under surface of the prothallium (Fig. 111, *A*), and differ from those of all Bryophytes, except the *Anthoceros* forms, in being sunk in the tissue of the prothallium and opening on the sur-

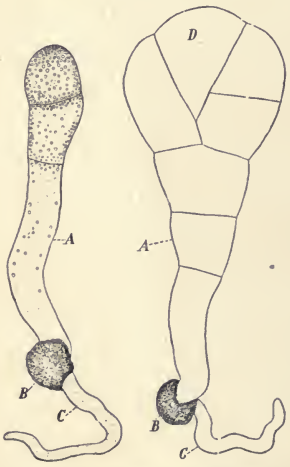


Fig. 115. Development of gametophyte of *Pteris;* the figure to the left shows the old spore (*B*), the rhizoid (*C*), and the thallus (*A*); that to the right is older, showing the same parts, and also the apical cell (*D*).—Caldwell.

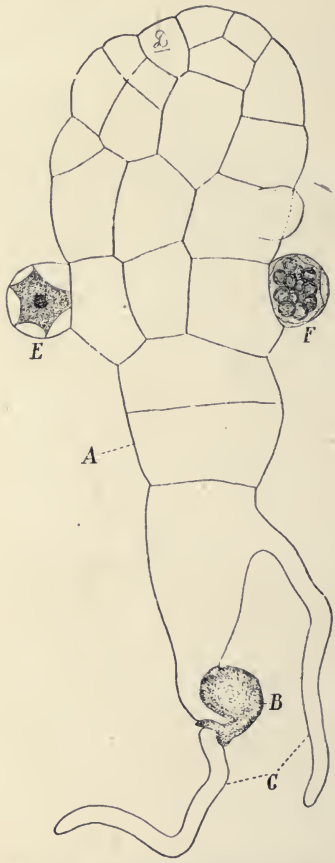


Fig. 116. Young gametophyte of *Pteris*, showing old spore wall (*B*), rhizoids (*C*), apical cell (*D*), a young anther idium (*E*), and an older one in which sperms have organized (*F*).—Caldwell.

face, more or less of the neck of the archegonium projecting (Fig. 113). The eggs are not different from those formed within the archegonia of Bryophytes, but the sperms are very different. The Bryophyte sperm has a small body and two long cilia, while the Pteridophyte sperm has a long spirally coiled body, blunt behind and tapering to a point in front, where numerous cilia are developed (Fig. 114). It is, therefore, a large, spirally-coiled, multiciliate sperm, and is quite characteristic of all Pteridophytes excepting the Club-mosses. It is evident that a certain amount of water is necessary for fertilization—in fact, it is needed not only

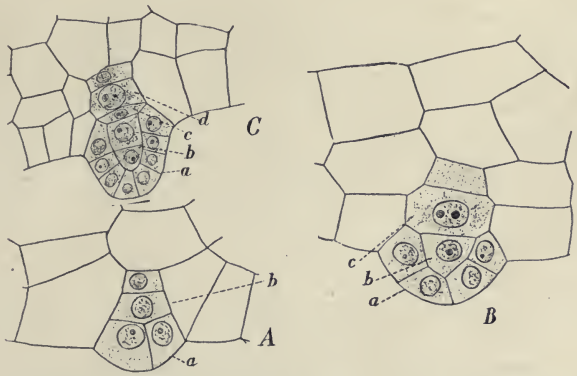


FIG. 117. Sections of portions of the gametophyte of *Pteris*, showing development of archegonium: *A*, young stage, showing cells which develop the neck (*a*), and the cell from which the egg cell and canal cells develop (*b*); *B*, an older stage, showing neck cells (*a*), neck canal cell (*b*), and cell from which is derived the egg cell, and the ventral canal cell (*c*); *C*, a still older stage, showing increased number of neck cells (*a*), two neck canal cells (*b*), the ventral canal cell (*c*), and the cell in which the egg is organized (*d*).—CALDWELL.

by the swimming sperm, but also to cause the opening of the antheridium and of the archegonium neck. There seems to be a relation between the necessity of water for fertilization and a prostrate, easily moistened gametophyte.

Prothallia are either monœcious or diœcious (see § 69). When the prothallia are developing (Fig. 115) the anther-

FIG. 118. A fern (*Aspidium*), showing three large branching leaves coming from a horizontal subterranean stem (rootstock); young leaves are also shown, which show circinate vernation. The stem, young leaves, and petioles of the large leaves are thickly covered with protecting hairs. The stem gives rise to numerous small roots from its lower surface. The figure marked *3* represents the under surface of a portion of the leaf, showing seven sori with shield-like indusia; at *5* is represented a section through a sorus, showing the sporangia attached and protected by the indusium; while at *6* is represented a single sporangium opening and discharging its spores, the heavy annulus extending along the back and over the top.—After WOSSIDLO.

idia begin to appear very early (Fig. 116), and later the archegonia (Fig. 117). If the prothallium is poorly nourished, only antheridia appear; it needs to be well developed and nourished to develop archegonia. There seems to be a very definite relation, therefore, between nutrition and the development of the two sex organs, a fact which must be remembered in connection with certain later developments.

79. **The sporophyte.**—This complex body is differentiated into root, stem, and leaf, and is more highly organized than any plant body heretofore mentioned (Fig. 118). The development of this body and its three great working regions must be considered separately.

(1) *Development of embryo.*—The oospore, from which the sporophyte develops, rests in the venter of the archegonium, which at this stage resembles a depression in the

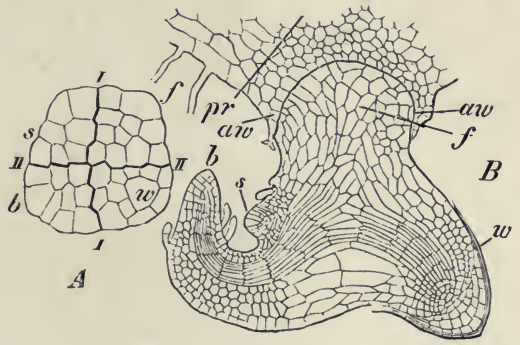


Fig. 119. Embryos of a common fern (*Pteris*): *A*, young embryo, showing direction of basal wall (*I*), and of second walls (*II*), which organize quadrants, each of which subsequently develops into foot (*f*), root (*w*), leaf (*b*), and stem (*s*); *B*, an older embryo, in which the four regions (lettered as in *A*) have developed further, also showing venter of archegonium (*aw*), and some tissue of the prothallium (*pr*). —*A* after Kienitz-Gerloff; *B* after Hofmeister.

lower surface of the prothallium (Fig. 119, *B*). It germinates at once, as in Bryophytes, not being a resting spore as in Green Algæ. The resting stage, as in the Bryophytes,

is in connection with the asexual spores, which may be kept for a long time and then germinated.

The first step in germination is for the oospore to divide into two cells, forming a two-celled embryo. In the ordinary Ferns this first dividing wall is at right angles to the surface of the prothallium, and is called the *basal wall* (Fig. 119, *A*). One of the two cells, therefore, is anterior (toward the notch of the prothallium), and the other is posterior.

The two cells next divide by forming walls at right angles to the basal wall, and a four-celled embryo is the result. This is called the "quadrant stage" of the embryo, as each one of the four cells is like the quadrant of a sphere.

With the appearance of the quadrant, four body regions are organized, each cell by its subsequent divisions giving rise to a distinct working region (Fig. 119, *A*). Two of the cells are inner (away from the substratum); also one of the inner and one of the outer (toward the substratum) cells are anterior; while the two other inner and outer cells are posterior. The anterior outer cell develops the first leaf of the embryo, generally called the *cotyledon* (Fig. 119, *b*); the anterior inner cell develops the stem (Fig. 119, *s*); the posterior outer cell develops the first (primary) root (Fig. 119, *w*); the posterior inner cell develops a special organ for the use of the embryo, called the *foot* (Fig. 119, *f*). The foot remains in close contact with the prothallium and absorbs nourishment from it for the young embryo. When the young sporophyte has developed enough to become independent the foot disappears. It is therefore spoken of as a temporary organ of the embryo. It is necessary for the leaf to emerge from beneath the prothallium, and it may be seen usually curving upward through the notch. The other parts remain subterranean.

(2) *The root.*—The primary root organized by one of the quadrants of the embryo is a temporary affair (Figs.

111, 119), as it is in an unfavorable position in reference to the dorsiventral stem, which puts out a series of more favorably placed secondary roots into the soil (Fig. 118). The mature leafy sporophyte, therefore, has neither foot nor primary root, the product of two of the quadrants of the embryo having disappeared.

The secondary roots put out by the stem are small, and do not organize an extensive system, but they are interesting as representing the first appearance of true roots, which therefore come in with the vascular system. In the lower groups the root function of absorption is conducted by simple hair-like processes called rhizoids; but true roots are complex in structure and contain vessels.

(3) *The stem.*—In most of the Ferns the stem is subterranean and dorsiventral (Fig. 118), but in the "tree ferns" of the tropics it forms an erect, aërial shaft bearing a crown of leaves (Fig. 120). In the other groups of Pteridophytes there are also aërial stems, both erect and prostrate. The stem is complex in structure, the cells being organized into different "tissue systems," prominent among which is the vascular system. These tissue systems of vascular plants are described in Chapter XV.

The appearance of the vascular system in connection with the leafy sporophyte is worthy of note. The leaves are special organs for chlorophyll work, and must receive the raw material from air and soil or water. The leaves of the moss gametophyte are very small and simple affairs, and can be supplied with material by using very little apparatus. In the leafy sporophyte, however, the leaves are very prominent structures, capable of doing a great deal of work. To such working structures material must be brought rapidly in quantity, and manufactured food material must be carried away, and therefore a special conducting apparatus is needed. This is supplied by the vascular system. These vessels extend continuously from root-tips, through the stem, and out into the leaves, where they

FIG. 120. A group of tropical plants. To the left of the center is a tree fern, with its slender columnar stem and crown of large leaves. The large-leaved plants to the right are bananas (Monocotyledons).—From "Plant Relations."

are spoken of as "leaf veins." Large working leaves and a vascular system, therefore, belong together and appear together; and the vascular plants are also the plants with leafy sporophytes.

(4) *The leaf.*—Leaves are devices for spreading out green tissue to the light, and in the Ferns they are usually large. There is a stalk-like portion (*petiole*) which rises from the subterranean stem, and a broad expanded portion (*blade*) exposed to the light and air (Fig. 118). In Ferns the blade is usually much branched, being cut up into segments of various sizes and forms.

The essential structure consists of an expansion of green tissue (*mesophyll*), through which strands of the vascular system (*veins*) branch, forming a supporting framework, and over all a compact layer of protecting cells (*epidermis*). A surface view of the epidermis shows that it is pierced by numerous peculiar pores, called *stomata*, meaning "mouths." The surface view of a stoma shows two crescentic cells (*guard cells*) in contact at the ends and leaving between them a lens-shaped opening (Fig. 121).

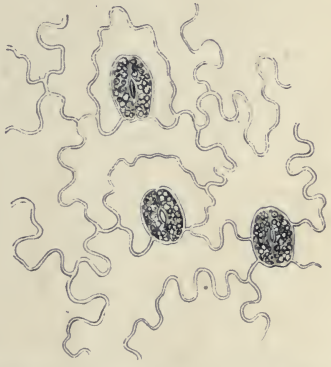


Fig. 121. Some epidermal cells from leaf of *Pteris*, showing the interlocking walls and three stomata, the guard cells containing chloroplasts.—Caldwell.

A cross-section through a leaf gives a good view of the three regions (Fig. 122). Above and below is the colorless epidermis, pierced here and there by stomata; between the epidermal layers the cells of the mesophyll are packed; and among the mesophyll cells there may be seen here and there the cut ends of the veins. The leaf is usually a dorsiventral

organ, its two surfaces being differently related to light. To this different relation the mesophyll cells respond in their arrangement. Those in contact with the upper epidermis become elongated and set endwise close together, forming the *palisade tissue;* those below are loosely ar-

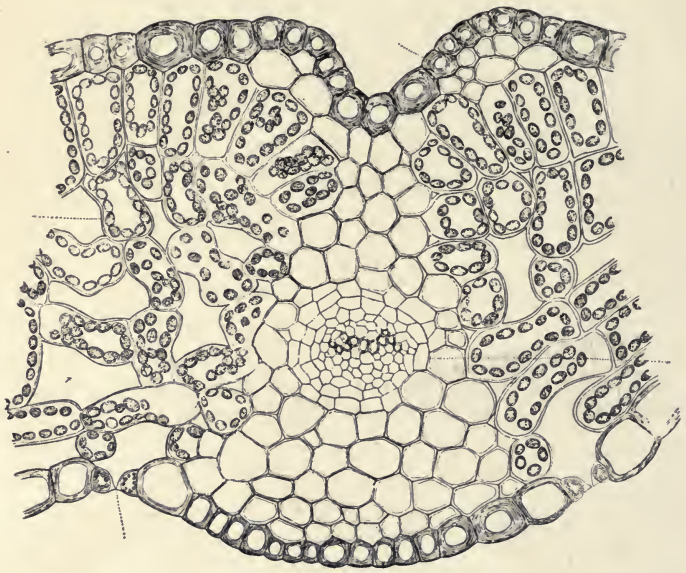


Fig. 122. Cross-section through a portion of the leaf of *Pteris*, showing the heavy-walled epidermis above and below, two stomata in the lower epidermis (one on each side of the center) opening into intercellular passages, the mesophyll cells containing chloroplasts, the upper row arranged in palisade fashion, the other cells loosely arranged (spongy mesophyll) and leaving large intercellular passages, and in the center a section of a veinlet (vascular bundle), the xylem being represented by the central group of heavy-walled cells.—Caldwell.

ranged, leaving numerous intercellular spaces, forming the *spongy tissue.* These spaces form a system of intercellular passageways among the working mesophyll cells, putting them into communication with the outer air through the stomata. The freedom of this communication

is regulated by the guard cells of the stomata, which come together or shrink apart as occasion requires, thus diminishing or enlarging the opening between them. The stomata have well been called "automatic gateways" to the system of intercellular passageways.

One of the peculiarities of ordinary fern leaves is that the vein system branches dichotomously, the forking veins being very conspicuous (Figs. 123–126). Another fern habit is that the leaves in expanding seem to unroll from the base, as though they had been rolled from the apex downward, the apex being in the center of the roll (Fig. 118). This habit is spoken of as *circinate*, from a word meaning "circle" or "coil," and circinate leaves when unrolling have a crozier-like tip. The arrangement of leaves in bud is called *vernation* ("spring condition"), and therefore the Ferns are said to have circinate vernation. The combination of dichotomous venation and circinate vernation is very characteristic of Ferns.

80. **Sporangia.**—Among Thallophytes sporangia are usually simple, mostly consisting of a single mother cell; among Bryophytes simple sporangia do not exist, and in connection with the usually complex capsule of the sporogonium the name is dropped; but among Pteridophytes distinct sporangia again appear. They are not simple mother cells, but many-celled bodies. Their structure varies in different groups of Pteridophytes, but those of ordinary Ferns may be taken as an illustration.

The sporangia are borne by the leaves, generally upon the under surface, and are usually closely associated with the veins and organized into groups of definite form, known as *sori*. A sorus may be round or elongated, and is usually covered by a delicate flap (*indusium*) which arises from the epidermis (Figs. 118, 123, 124). Occasionally the sori are extended along the under surface of the margin of the leaf, as in maidenhair fern (*Adiantum*), and the common brake (*Pteris*), in which case they are protected by the inrolled

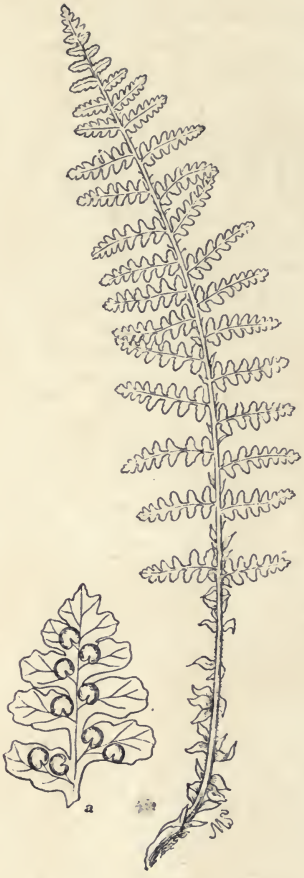


FIG. 123. Fragrant shield fern (*Aspidium fragrans*), showing general habit, and to the left (*a*) the under surface of a leaflet bearing sori covered by shield-like indusia.—After MARION SATTERLEE.

FIG. 124. The bladder fern (*Cystopteris bulbifera*), showing general habit, and to the right (*a*) the under surface of a leaflet, showing the dichotomous venation, and five sori protected by pouch-like indusia. —After MARION SATTERLEE.

margin (Figs. 125, 126), which may be called a "false indusium."

It is evident that such leaves are doing two distinct kinds of work—chlorophyll work and spore formation. This is true of most of the ordinary Ferns, but some of them show a tendency to divide the work. Certain leaves, or certain leaf-branches, produce spores and do no chlorophyll work, while others do chlorophyll work and produce no spores. This differentiation in the leaves or leaf-regions is indicated by appropriate names. Those leaves which produce only spores are called *sporophylls*, meaning "spore leaves," while the leaf branches thus set apart are called sporophyll branches. Those leaves which only do chlorophyll work are called *foliage leaves;* and such branches are foliage branches. As sporophylls are not called upon for chlorophyll work they often become much modified, being much more compact, and not at all resembling the foliage leaves. Such a differentiation may be seen in the ostrich fern and sensitive fern (*Onoclea*) (Figs. 127, 128), the climbing fern (*Lygodium*), the royal fern (*Osmunda*), the moonwort (*Botrychium*) (Fig. 129), and the adder's tongue (*Ophioglossum*) (Fig. 130).

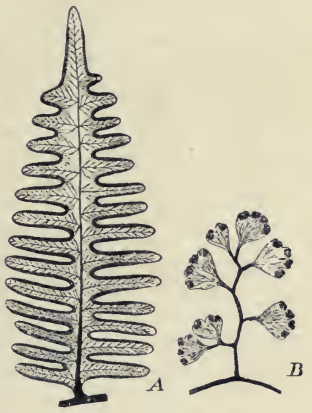


FIG. 125. Leaflets of two common ferns: *A*, the common brake (*Pteris*); *B*, maidenhair (*Adiantum*); both showing sori borne at the margin and protected by the infolded margin, which thus forms a false indusium.—CALDWELL.

An ordinary fern sporangium consists of a slender stalk and a bulbous top which is the spore case (Fig. 118, *6*). This case has a delicate wall formed of a single layer of cells, and extending around it from the stalk and nearly to

the stalk again, like a meridian line about a globe, is a row of peculiar cells with thick walls, forming a heavy ring, called the *annulus*. The annulus is like a bent spring, and when the delicate wall becomes yielding the spring straightens violently, the wall is torn, and the spores are discharged with considerable force (Fig. 131). This dis-

FIG. 126.—The purple cliff brake (*Pellæa atropurpurea*), showing general habit, and at *a* a single leaflet showing the dichotomous venation and the infolded margin covering the sori.—After MARION SATTERLEE.

charge of fern spores may be seen by placing some sporangia upon a moist slide, and under a low power watching them as they dry and burst.

Within this sporangium the archesporium (see § 66) consists of a single cell, which by division finally produces

numerous mother cells, in each of which a tetrad of spores is formed. The disorganization of the walls of the mother

FIG. 127. The ostrich fern (*Onoclea struthiopteris*), showing differentiation of foliage leaf (*a*) and sporophyll (*b*).—After MARION SATTERLEE.

cells sets the spores free in the cavity of the sporangium, and ready for discharge.

FIG. 128. The sensitive fern (*Onoclea sensibilis*), showing differentiation of foliage leaves and sporophylls.—From "Field, Forest, and Wayside Flowers."

Among the Bryophytes the sporogenous tissue appears very early in the development of the sporogonium, the production of spores being its only function; also there is a

Fig. 129. A moonwort (*Botrychium*), showing the leaf differentiated into foliage and sporophyll branches.—After Strasburger.

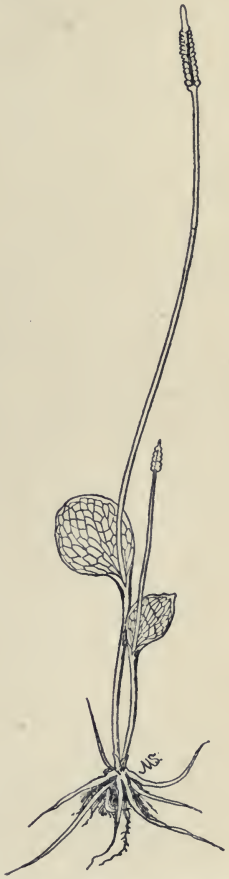


Fig. 130. The adder's tongue (*Ophioglossum vulgatum*), showing two leaves, each with a foliage branch and a much longer sporophyll branch.—After Marion Satterlee.

tendency to restrict the sporogenous tissue and increase the sterile tissue. It will be observed that with the introduction of the leafy sporophyte among the Pteridophytes the sporangia appear much later in its development, sometimes not appearing for several years, as though they are of

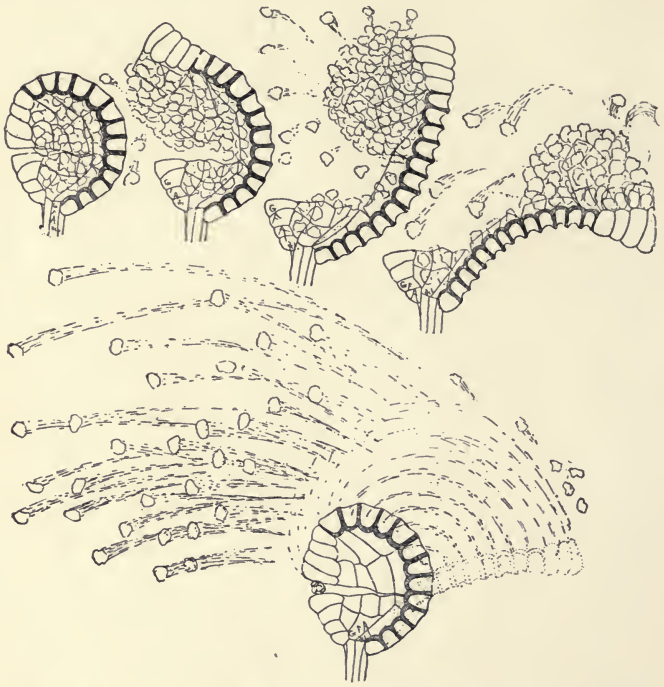


Fig. 131. A series showing the dehiscence of a fern sporangium, the rupture of the wall, the straightening and bending back of the annulus, and the recoil.—After Atkinson.

secondary importance as compared with chlorophyll work; and that the sporogenous tissue is far more restricted, the sporangia forming a very small part of the bulk of the sporophyte body.

81. **Heterospory.**—This phenomenon appears first among Pteridophytes, but it is not characteristic of them, being entirely absent from the true Ferns, which far outnumber all other Pteridophytes. Its chief interest lies in the fact that it is universal among the Spermatophytes, and that it represents the change which leads to the appearance of that high group. It is impossible to understand the greatest group of plants, therefore, without knowing something about heterospory. As it begins in simple fashion among Pteridophytes, and is probably the greatest contribution they have made to the evolution of the plant kingdom, unless it be the leafy sporophyte, it is best explained here.

In the ordinary Ferns all the spores in the sporangia are alike, and when they germinate each spore produces a prothallium upon which both antheridia and archegonia appear. It has been remarked, however, that some prothallia are diœcious—that is, some bear only antheridia and others bear only archegonia. In this case it is evident that the spores in the sporangium, although they may appear alike, produce different kinds of prothallia, which may be called male and female, as each is distinguished by the sex organ which it produces. As archegonia are only produced by well-nourished prothallia, it seems fair to suppose that the larger spores will produce female prothallia, and the smaller ones male prothallia.

This condition of things seems to have developed finally into a permanent and decided difference in the size of the spores, some being quite small and others relatively large, the small ones producing male gametophytes (prothallia with antheridia), and the large ones female gametophytes (prothallia with archegonia). When asexual spores differ thus permanently in size, and give rise to gametophytes of different sexes, we have the condition called *heterospory* ("spores different"), and such plants are called *heterosporous* (Fig. 139). In contrast with heterosporous plants, those in which the asexual spores appear alike are called *homos-*

porous, or sometimes *isosporous,* both terms meaning "spores similar." The corresponding noun form is *homospory* or *isospory.* Bryophytes and most Pteridophytes are homosporous, while some Pteridophytes and all Spermatophytes are heterosporous.

It is convenient to distinguish by suitable names the two kinds of asexual spores produced by the sporangia of heterosporous plants (Fig. 139). The large ones are called *megaspores,* or by some writers *macrospores,* both terms meaning "large spores"; the small ones are called *microspores,* or "small spores." It should be remembered that megaspores always produce female gametophytes, and microspores male gametophytes.

This differentiation does not end with the spores, but soon involves the sporangia (Fig. 139). Some sporangia produce only megaspores, and are called *megasporangia;* others produce only microspores, and are called *microsporangia.* It is important to note that while microsporangia usually produce numerous microspores, the megasporangia produce much fewer megaspores, the tendency being to diminish the number and increase the size, until finally there are megasporangia which produce but a single large megaspore.

The differentiation goes still further. If the sporangia are born upon sporophylls, the sporophylls themselves may differentiate, some bearing only megasporangia, and others only microsporangia, the former being called *megasporophylls,* the latter *microsporophylls.* In such a case the sequence is as follows: megasporophylls produce megasporangia, which produce megaspores, which in germination produce the female gametophytes (prothallia with archegonia); while the microsporophylls produce microsporangia, which produce microspores, which in germination produce male gametophytes (prothallia with antheridia).

A formula may indicate the life history of a heterosporous plant. The formula of homosporous plants with

alternation of generations (Bryophytes and most Pteridophytes) was given as follows (§ 62):

$$G\begin{smallmatrix}-o\\-o\end{smallmatrix}>o-S-o-G\begin{smallmatrix}-o\\-o\end{smallmatrix}>o-S-o-G\begin{smallmatrix}-o\\-o\end{smallmatrix}>o-S, \text{ etc.}$$

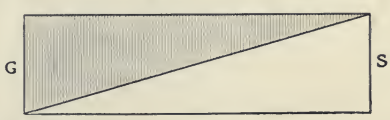
In the case of heterosporous plants (some Pteridophytes and all Spermatophytes) it would be modified as follows:

$$\begin{smallmatrix}G-o\\G-o\end{smallmatrix}>o-S\begin{smallmatrix}-o-G-o\\-o-G-o\end{smallmatrix}>o-S\begin{smallmatrix}-o-G-o\\-o-G-o\end{smallmatrix}>o-S, \text{ etc.}$$

In this case two gametophytes are involved, one producing a sperm, the other an egg, which fuse and form the oospore, which in germination produces the sporophyte, which produces two kinds of asexual spores (megaspores and microspores), which in germination produce the two gametophytes again.

One additional fact connected with heterospory should be mentioned, and that is the great reduction of the gametophyte. In the homosporous ferns the spore develops a small but free and independent prothallium which produces both sex organs. When in heterosporous plants this work of producing sex organs is divided between two gametophytes they become very much reduced in size and lose their freedom and independence. They are so small that they do not escape entirely, if at all, from the embrace of the spores which produce them, and are mainly dependent for their nourishment upon the food stored up in the spores (Figs. 140, 141). As the spore is produced by the sporophyte, heterospory brings about a condition in which the gametophyte is dependent upon the sporophyte, an exact reversal of the condition in Bryophytes.

The relative importance of the gametophyte and the sporophyte throughout the plant kingdom may be roughly indicated by the accompanying diagram, in which the



shaded part of the parallelogram represents the gametophyte and the unshaded part the sporophyte. Among the

lowest plants the gametophyte is represented by the whole plant structure. When the sporophyte first appears it is dependent upon the gametophyte (some Thallophytes and the Bryophytes), and is relatively inconspicuous. Later the sporophyte becomes independent (most Pteridophytes), the gametophyte being relatively inconspicuous. Finally (heterosporous Pteridophytes) the gametophyte becomes dependent upon the sporophyte, and in Spermatophytes is so inconspicuous and concealed that it is only observed by means of laboratory appliances, while the sporophyte is the whole plant of ordinary observation.

CHAPTER X

THE GREAT GROUPS OF PTERIDOPHYTES

82. **The great groups.**—At least three independent lines of Pteridophytes are recognized: (1) *Filicales* (Ferns), (2) *Equisetales* (Scouring rushes, Horsetails), and (3) *Lycopodiales* (Club-mosses). The Ferns are much the most abundant, the Club-mosses are represented by a few hundred forms, while the Horsetails include only about twenty-five species. These three great groups are so unlike that they hardly seem to belong together in the same division of the plant kingdom.

Filicales (*Ferns*)

83. **General characters.**—The Ferns were used in the preceding chapter as types of Pteridophytes, so that little need be added. They well deserve to stand as types, as they contain about four thousand of the four thousand five hundred species belonging to Pteridophytes. Although found in considerable numbers in temperate regions, their chief display is in the tropics, where they form a striking and characteristic feature of the vegetation. In the tropics not only are great masses of the low forms to be seen, from those with delicate and filmy moss like leaves to those with huge leaves, but also tree forms with cylindrical trunks encased by the rough remnants of fallen leaves and sometimes rising to a height of thirty-five to forty-five feet, with a great crown of leaves fifteen to twenty feet long (Fig. 120).

FIG. 132. A bank of ferns (*Osmunda Claytoniana*).—CALDWELL.

There are also *epiphytic* forms (air plants)—that is, those which perch "upon other plants" but derive no nourishment from them (Fig. 112). This habit belongs chiefly to the warm and moist tropics, where the plants can absorb sufficient moisture from the air without sending roots into the soil. In this way many of the tropical ferns are found growing upon living and dead trees and other plants. In the temperate regions the chief epiphytes are Lichens, Liverworts, and Mosses, the Ferns being chiefly found in moist woods and ravines (Fig. 132), although a number grow in comparatively dry and exposed situations, sometimes covering extensive areas, as the common brake (*Pteris*) (Fig. 125).

The Filicales differ from the other groups of Pteridophytes chiefly in having few large leaves, which do chlorophyll work and bear sporangia. In a few of them there is a differentiation of functions in foliage branches and sporophyll branches (Figs. 127–130), but even this is exceptional. Another distinction is that the stems are unbranched.

84. **Origin of sporangia.**—An important feature in the Ferns is the origin of the sporangia. In some of them a sporangium is developed from a single epidermal cell of the leaf, and is an entirely superficial and generally stalked affair (Fig. 118, *5*) ; in others the sporangium in its development involves several epidermal and deeper cells of the leaf, and is more or less of an imbedded affair. In the first case the ferns are said to be *leptosporangiate ;* in the second case they are *eusporangiate.*

The leptosporangiate Ferns are overwhelmingly abundant as compared with the Eusporangiates. Back in the Coal-measures, however, there was an abundant fern vegetation which was probably all eusporangiate. The Leptosporangiates seem to be the modern Ferns, the once abundant Eusporangiates being represented now in the temperate regions only by such forms as moonwort (*Bo-*

trychium) (Fig. 129) and adder's tongue (*Ophioglossum*) (Fig. 130). It is important to note, however, that the Horsetails and Club-mosses are Eusporangiates, as well as all the Seed-plants.

Another small but interesting group of Ferns includes the "Water-ferns," floating forms or sometimes on muddy flats. The common *Marsilia* may be taken as a type (Fig. 133). The slender creeping stem sends down numerous roots into the mucky soil, and at intervals gives rise to a comparatively large leaf. This leaf has a long erect petiole and a blade of four spreading wedge-shaped leaflets like a "four-leaved clover." The dichotomous venation and circinate vernation at once suggest the fern alliance. From near the base of the petiole

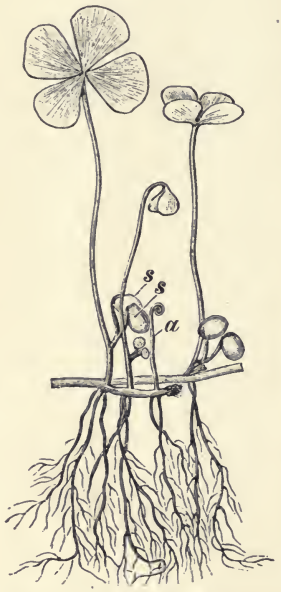


FIG. 133.—A water-fern (*Marsilia*), showing horizontal stem, with descending roots, and ascending leaves; *a*, a young leaf showing circinate vernation; *s*, *s*, sporophyll branches ("sporocarps").—After BISCHOFF.

FIG. 134. One of the floating water-ferns (*Salvinia*), showing side view (*A*) and view from above (*B*). The dangling root-like processes are the modified submerged leaves. In *A*, near the top of the cluster of submerged leaves, some sporophyll branches ("sporocarps") may be seen.—After BISCHOFF.

another leaf branch arises, in which the blade is modified as a sporophyll. In this case the sporophyll incloses the sporangia and becomes hard and nut-like. Another common form is the floating *Salvinia* (Fig. 134). The chief interest lies in the fact that the water-ferns are heterosporous. As they are leptosporangiate they are thought to have been derived from the ordinary leptosporangiate Ferns, which are homosporous.

Three fern groups are thus outlined: (1) homosporous-eusporangiate forms, now almost extinct; (2) homosporous-leptosporangiate forms, the great overwhelming modern group, not only of Filicales but also of Pteridophytes, well called true Ferns, and thought to be derived from the preceding group; and (3) heterosporous-leptosporangiate forms, the water-ferns, thought to be derived from the preceding group.

Equisetales (*Horsetails or Scouring rushes*)

85. **General characters.**—The twenty-five forms now representing this great group belong to a single genus (*Equisetum*, meaning "horsetail"), but they are but the lingering remnants of an abundant flora which lived in the time of the Coal-measures, and helped to form the forest vegetation. The living forms are small and inconspicuous, but very characteristic in appearance. They grow in moist or dry places, sometimes in great abundance (Fig. 135).

The stem is slender and conspicuously jointed, the joints separating easily; it is also green and fluted with small longitudinal ridges; and there is such an abundant deposit of silica in the epidermis that the plants feel rough. This last property suggested its former use in scouring, and its name "scouring rush." At each joint is a sheath of minute leaves, more or less coalesced, the individual leaves sometimes being indicated only by minute teeth. This arrangement of leaves in a circle about the joint is called the *cyclic*

Fig. 135. *Equisetum arvense*, a common horsetail: *1*, three fertile shoots rising from the dorsiventral stem, showing the cycles of coalesced scale-leaves at the joints and the terminal strobili with numerous sporophylls, that at *a* being mature; *2*, a sterile shoot from the same stem, showing branching; *3*, a single peltate sporophyll bearing sporangia; *4*, view of sporophyll from beneath, showing dehiscence of sporangia; *5*, *6*, *7*, spores, showing the unwinding of the outer coat, which aids in dispersal.—After Wossidlo.

arrangement, or sometimes the *whorled* arrangement, each such set of leaves being called a *cycle* or a *whorl*. These leaves contain no chlorophyll and have evidently abandoned chlorophyll work, which is carried on by the green stem. Such leaves are known as *scales*, to distinguish them from foliage leaves. The stem is either simple or profusely branched (Fig. 135).

86. **The strobilus.**—One of the distinguishing characters of the group is that chlorophyll-work and spore-formation are completely differentiated. Although the foliage leaves

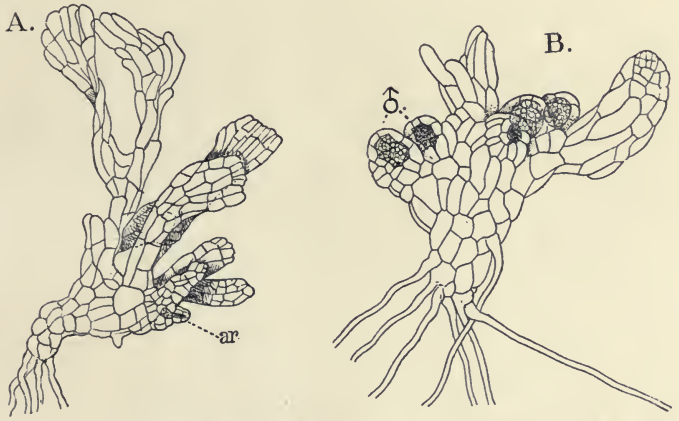


Fig. 136. Dicœcious gametophytes of *Equisetum*: *A*, the female gametophyte, showing branching, rhizoids, and an archegonium (*ar*); *B*, the male gametophyte, showing several antheridia (♂).—After Campbell.

are reduced to scales, and the chlorophyll-work is done by the stem, there are well-organized sporophylls. The sporophylls are grouped close together at the end of the stem in a compact conical cluster which is called a *strobilus*, the Latin name for "pine cone," which this cluster of sporophylls resembles (Fig. 135).

Each sporophyll consists of a stalk-like portion and a shield-like (*peltate*) top. Beneath the shield hang the

sporangia, which produce spores of but one kind, hence these plants are homosporous; and as the sporangia originate in eusporangiate fashion, *Equisetum* has the homosporous-eusporangiate combination shown by one of the Fern groups. It is interesting to know, however, that some of the ancient, more highly organized members of this group were heterosporous, and that the present forms have diœcious gametophytes (Fig. 136).

Lycopodiales (*Club-mosses*)

87. **General characters.**—This group is now represented by about five hundred species, most of which belong to the two genera *Lycopodium* and *Selaginella*, the latter being much the larger genus. The plants have slender, branching, prostrate, or erect stems completely clothed with small foliage leaves, having a general moss-like appearance (Fig. 137). Often the erect branches are terminated by conspicuous conical or cylindrical strobili, which are the "clubs" that enter into the name "Club-mosses." There is also a certain kind of resemblance to miniature pines, so that the name "Ground-pines" is sometimes used.

Lycopodiales were once much more abundant than now, and more highly organized, forming a conspicuous part of the forest vegetation of the Coal-measures.

One of the distinguishing marks of the group is that the sperm does not resemble that of the other Pteridophytes, but is of the Bryophyte type (Fig. 140, *F*). That is, it consists of a small body with two cilia, instead of a large spirally coiled body with many cilia. Another distinguishing character is that there is but a single sporangium produced by each sporophyll (Fig. 137). This is in marked contrast with the Filicales, whose leaves bear very numerous sporangia, and with the Equisetales, whose sporophylls bear several sporangia.

FIG. 137. A common club-moss (*Lycopodium clavatum*): *1*, the whole plant, showing horizontal stem giving rise to roots and to erect branches bearing strobili; *2*, a single sporophyll with its sporangium; *3*, spores, much magnified.—After WOSSIDLO.

88. **Lycopodium.**—This genus contains fewer forms than the other, but they are larger and coarser and more characteristic of the temperate regions, being the ordinary Club-mosses (Fig. 137). They also more commonly display conspicuous and distinct strobili, although there is every

gradation between ordinary foliage leaves and distinct sporophylls.

The sporangia are borne either by distinct sporophylls or by the ordinary foliage leaves near the summit of the stem. At the base of each of these leaves, or sporophylls, on the upper side, is a single sporangium (Fig. 137). The sporangia are eusporangiate in origin, and as the spores are all alike, *Lycopodium* has the same homosporous-eusporangiate combination noted in Equisetales and in one of the groups of Filicales.

89. **Selaginella.**—This large genus contains the smaller, more delicate Club-mosses, often being called the "little Club-mosses." They are especially displayed in the trop-

FIG. 138. *Selaginella*, showing general spray-like habit, and dangling leafless stems which strike root (*rhizophores*).—From "Plant Relations."

ics, and are common in greenhouses as delicate, mossy, decorative plants (Fig. 138). In general the sporophylls are not different from the ordinary leaves (Fig. 139), but sometimes they are modified, though not so distinct as in certain species of *Lycopodium*,

The solitary sporangium appears in the *axils* (upper angles formed by the leaves with the stem) of the leaves and sporophylls, but arise from the stem instead of the

FIG. 139. *Selaginella Martensii: A*, branch bearing strobili; *B*, a microsporophyll with a microsporangium, showing microspores through a rupture in the wall; *C*, a megasporophyll with a megasporangium; *D*, megaspores; *E*, microspores.—CALDWELL.

leaf (Fig. 139). This is important as showing that sporangia may be produced by stems as well as by leaves, those being produced by leaves being called *foliar*, and those by stem *cauline*.

The most important fact in connection with *Selaginella*, however, is that it is heterosporous. Megasporangia, each usually containing but four megaspores, are found in the axils of a few of the lower leaves of the strobilus, and more numerous microsporangia occur in the upper axils, containing very many microspores (Fig. 139). The character of the gametophytes of heterosporous Pteridophytes may be well illustrated by those of *Selaginella*.

The microspore germinates and forms a male gametophyte so small that it is entirely included within the spore

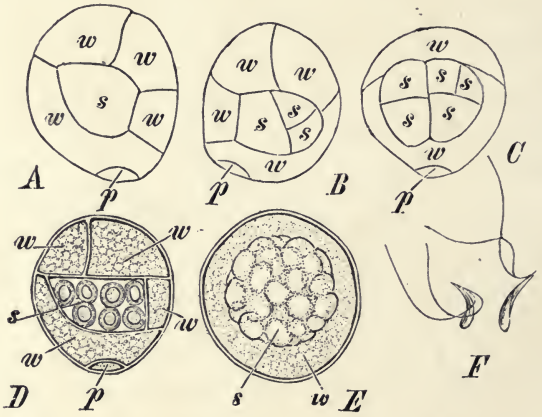


FIG. 140. Male gametophyte of *Selaginella*: in each case *p* is the prothallial cell, *w* the wall cells of the antheridium, *s* the sperm tissue: *F*, the biciliate sperms.—After BELAJEFF.

wall (Fig. 140). A single small cell is all that represents the ordinary cells of the prothallium, while all the rest is an antheridium, consisting of a wall of a few cells surrounding numerous sperm mother cells. In the presence

of water the antheridium wall breaks down, as also do the walls of the mother cells, and the small biciliate sperms are set free.

The much larger megaspores germinate and become filled with a mass of numerous nutritive cells, representing the ordinary cells of a prothallium (Fig. 141). The spore wall is broken by this growing prothallium, a part of which thus protrudes and becomes exposed, although the main part of it is still invested by the old megaspore wall. In this exposed portion of the female gametophyte the archegonia appear, and thus become accessible to the sperms. In the case of *Isoetes* (see § 90) the reduction of the female gametophyte is even greater, as it does not project from the megaspore wall at all, and the archegonia are made accessible through cracks in the wall immediately over them.

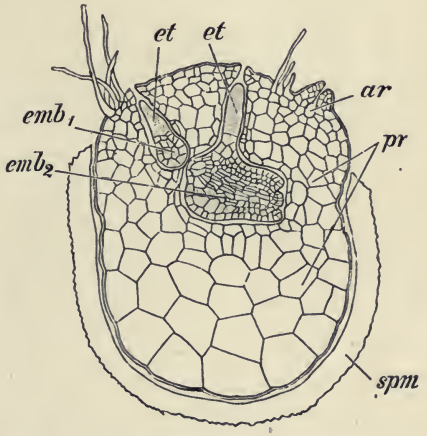


FIG. 141. Female gametophyte of a *Selaginella*: *spm*, wall of megaspore; *pr*, gametophyte; *ar*, an archegonium; emb_1 and emb_2, embryo sporophytes; *et*, suspensors; the gametophyte has developed a few rhizoids.—After PFEFFER.

The embryo of *Selaginella* is also important to consider. Beginning its development in the venter of the archegonium, it first lies upon the exposed margin of the prothallium, while the mass of nutritive cells lie deep within the megaspore (Fig. 141, emb_1, emb_2). It first develops an elongated cell, or row of cells, which thrusts the embryo cell deeper among the nutritive cells. This cell or row of cells, formed by the embryo to place the real embryo cell in better rela-

tion to its food supply, is called the *suspensor*, and is a temporary organ of the embryo (Figs. 141, 142, *et*). At the end of the suspensor the real embryo develops, and when its regions become organized it shows the following parts: (1) a large foot buried among the nutritive cells of the prothallium and absorbing nourishment; (2) a root stretching out toward the substratum; (3) a stem extend-

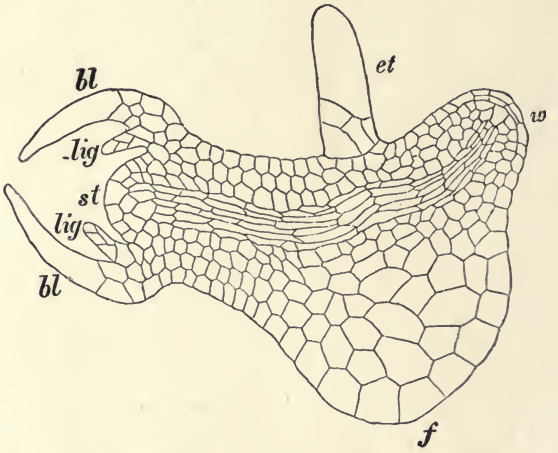


FIG. 142. Embryo of *Selaginella* removed from the gametophyte, showing suspensor (*et*), root-tip (*w*), foot (*f*), cotyledons (*bl*), stem-tip (*st*), and ligules (*lig*).—After PFEFFER.

ing in the other direction, and bearing just behind its tip (4) a pair of opposite leaves (cotyledons) (Fig. 142).

As the sporangia of *Selaginella* are eusporangiate, this genus has the heterosporous-eusporangiate combination—a combination not mentioned heretofore, and being of special interest as it is the combination which belongs to all the Spermatophytes. For this and other reasons, *Selaginella* is one of the Pteridophyte forms which has attracted special attention, as possibly representing one of the ancestral forms of the Seed-plants.

90. **Isoetes.**—This little group of aquatic plants, known as "quillworts," is very puzzling as to its relationships among Pteridophytes. By some it is put with the Ferns, forming a distinct division of Filicales; by others it is put

FIG. 143. A common quillwort (*Isoetes lacustris*), showing cluster of roots dichotomously branching, and cluster of leaves each enlarged at base and inclosing a single sporangium.—After SCHENCK.

FIG. 144. Sperm of *Isoetes*, showing spiral body and seven long cilia arising from the beak.—After BELAJEFF.

with the Club-mosses, and is associated with *Selaginella*. It resembles a bunch of fine grass growing in shoal water or in mud, but the leaves enlarge at the base and overlap one another and the very short tuberous stem (Fig. 143). Within each enlarged leaf base a single sporangium is formed, and the cluster contains both megasporangia and microsporangia. The sporangia are eusporangiate, and therefore *Isoetes* shares with *Selaginella* the distinction of

having the heterosporous-eusporangiate combination, which is a feature of the Seed-plants.

The embryo is also peculiar, and is so suggestive of the embryo of the Monocotyledons (see § 114) among Seed-plants that some regard it as possibly representing the ancestral forms of that group of Spermatophytes. The peculiarity lies in the fact that at one end of the axis of the embryo is a root, and at the other the first leaf (cotyledon), while the stem tip rises as a lateral outgrowth. This is exactly the distinctive feature of the embryo of Monocotyledons.

The greatest obstacle in the way of associating these quillworts with the Club-mosses is the fact that their sperms are of the large and spirally coiled multiciliate type which belongs to Filicales and Equisetales (Fig. 144), and not at all the small biciliate type which characterizes the Club-mosses (Fig. 140). To sum up, the short unbranched stem with comparatively few large leaves, and the coiled multiciliate sperm, suggest Filicales; while the solitary sporangia and the heterosporous-eusporangiate character suggest *Selaginella*.

CHAPTER XI

SPERMATOPHYTES: GYMNOSPERMS

91. **Summary from Pteridophytes.**—In considering the important contributions of Pteridophytes to the evolution of the plant kingdom the following seem worthy of note:

(1) *Prominence of sporophyte and development of vascular system.*—This prominence is associated with the display of leaves for chlorophyll work, and the leaves necessitate the work of conduction, which is arranged for by the vascular system. This fact is true of the whole group.

(2) *Differentiation of sporophylls.*—The appearance of sporophylls as distinct from foliage leaves, and their organization into the cluster known as the strobilus, are facts of prime importance. This differentiation appears more or less in all the great groups, but the strobilus is distinct only in Horsetails and Club-mosses.

(3) *Introduction of heterospory and reduction of gametophytes.*—Heterospory appears independently in all of the three great groups—in the water-ferns among the Filicales, in the ancient horsetails among the Equisetales, and in *Selaginella* and *Isoetes* among Lycopodiales. All the other Pteridophytes, and therefore the great majority of them, are homosporous. The importance of the appearance of heterospory lies in the fact that it leads to the development of Spermatophytes, and associated with it is a great reduction of the gametophytes, which project little, if at all, from the spores which produce them.

92. **Summary of the four groups.**—It may be well in this connection to give certain prominent characters which will

serve to distinguish the four great groups of plants. It must not be supposed that these are the only characters, or even the most important ones in every case, but they are convenient for our purpose. Two characters are given for each of the first three groups—one a positive character which belongs to it, the other a negative character which distinguishes it from the group above, and becomes the positive character of that group.

(1) *Thallophytes.*—Thallus body, but no archegonia.

(2) *Bryophytes.*—Archegonia, but no vascular system.

(3) *Pteridophytes.*—Vascular system, but no seeds.

(4) *Spermatophytes.*—Seeds.

93. **General characters of Spermatophytes.**—This is the greatest group of plants in rank and in display. So conspicuous are they, and so much do they enter into our experience, that they have often been studied as "botany," to the exclusion of the other groups. The lower groups are not merely necessary to fill out any general view of the plant kingdom, but they are absolutely essential to an understanding of the structures of the highest group.

This great dominant group has received a variety of names. Sometimes they are called *Anthophytes*, meaning "Flowering plants," with the idea that they are distinguished by the production of "flowers." A flower is difficult to define, but in the popular sense all Spermatophytes do not produce flowers, while in another sense the strobilus of Pteridophytes is a flower. Hence the flower does not accurately limit the group, and the name Anthophytes is not in general use. Much more commonly the group is called *Phanerogams* (sometimes corrupted into Phænogams or even Phenogams), meaning "evident sexual reproduction." At the time this name was proposed all the other groups were called *Cryptogams*, meaning "hidden sexual reproduction." It is a curious fact that the names ought to have been reversed, for sexual reproduction is much more evident in Cryptogams than in Phanerogams, the mistake

arising from the fact that what were supposed to be sexual organs in Phanerogams have proved not to be such. The name Phanerogam, therefore, is being generally abandoned; but the name Cryptogam is a useful one when the lower groups are to be referred to; and the Pteridophytes are still very frequently called the *Vascular Cryptogams*. The most distinguishing mark of the group seems to be the production of seeds, and hence the name *Spermatophytes*, or "Seed-plants," is coming into general use.

The seed can be better defined after its development has been described, but it results from the fact that in this group the single megaspore is never discharged from its megasporangium, but germinates just where it is developed. The great fact connected with the group, therefore, is the retention of the megaspore, which results in a seed. The full meaning of this will appear later.

There are two very independent lines of Seed-plants, the *Gymnosperms* and the *Angiosperms*. The first name means "naked seeds," referring to the fact that the seeds are always exposed; the second means "inclosed seeds," as the seeds are inclosed in a seed vessel.

Gymnosperms

94. **General characters.**—The most familiar Gymnosperms in temperate regions are the pines, spruces, hemlocks, cedars, etc., the group so commonly called "evergreens." It is an ancient tree group, for its representatives were associated with the giant club-mosses and horsetails in the forest vegetation of the Coal-measures. Only about four hundred species exist to-day as a remnant of its former display, although the pines still form extensive forests. The group is so diversified in its structure that all forms can not be included in a single description. The common pine (*Pinus*), therefore, will be taken as a type, to show the general Gymnosperm character.

95. **The plant body.**—The great body of the plant, often forming a large tree, is the sporophyte; in fact, the gametophytes are not visible to ordinary observation. It should be remembered that the sporophyte is distinctly a sexless generation, and that it develops no sex organs. This great sporophyte body is elaborately organized for nutritive work, with its roots, stems, and leaves. These organs are very complex in structure, being made up of various tissue systems that are organized for special kinds of work. The leaves are the most variable organs, being differentiated into three distinct kinds—(1) foliage leaves, (2) scales, and (3) sporophylls.

96. **Sporophylls.**—The sporophylls are leaves set apart to produce sporangia, and in the pine they are arranged in a strobilus, as in the Horsetails and Club-mosses. As the group is heterosporous, however, there are two kinds of sporophylls and two kinds of strobili. One kind of strobilus is made up of megasporophylls bearing megasporangia; the other is made up of microsporophylls bearing microsporangia. These strobili are often spoken of as the "flowers" of the pine, but if these are flowers, so are the strobili of Horsetails and Club-mosses.

97. **Microsporophylls.**—In the pines the strobilus composed of microsporophylls is comparatively small (Figs. 145, *d*, 164). Each sporophyll is like a scale leaf, is narrowed at the base, and upon the lower surface are borne two prominent sporangia, which of course are microsporangia, and contain microspores (Fig. 146).

These structures of Seed-plants all received names before they were identified with the corresponding structures of the lower groups. The microsporophyll was called a *stamen*, the microsporangia *pollen-sacs*, and the microspores *pollen grains*, or simply *pollen*. These names are still very convenient to use in connection with the Spermatophytes, but it should be remembered that they are simply other names for structures found in the lower groups.

FIG. 145. *Pinus Laricio*, showing tip of branch bearing needle-leaves, scale-leaves, and cones (strobili): *a*, very young carpellate cones, at time of pollination, borne at tip of the young shoot upon which new leaves are appearing; *b*, carpellate cones one year old; *c*, carpellate cones two years old, the scales spreading and shedding the seeds; *d*, young shoot bearing a cluster of staminate cones.—CALDWELL.

The strobilus composed of microsporophylls may be called the *staminate strobilus*—that is, one composed of stamens; it is often called the staminate cone, "cone" being the English translation of the word "strobilus." Frequently the staminate cone is spoken of as the "male cone," as it was once supposed that the stamen is the

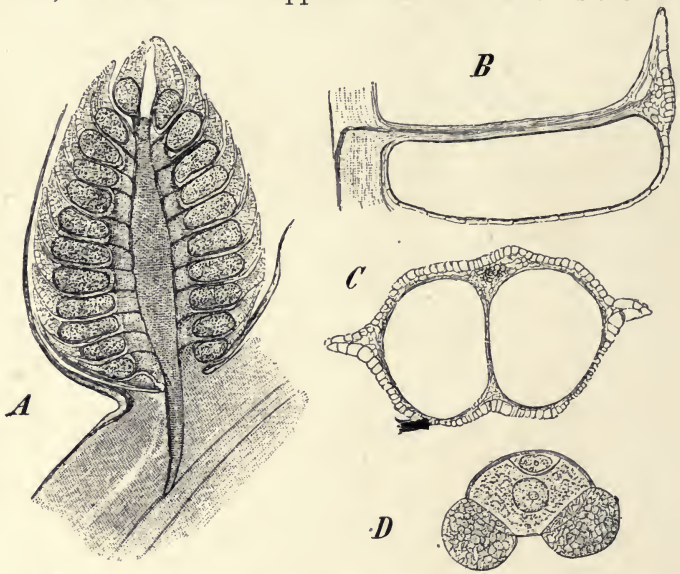


FIG. 146. Staminate cone (strobilus) of pine (*Pinus*): *A*, section of cone, showing microsporophylls (stamens) bearing microsporangia; *B*, longitudinal section of a single stamen, showing the large sporangium beneath; *C*, cross-section of a stamen, showing the two sporangia; *D*, a single microspore (pollen grain) much enlarged, showing the two wings, and a male gametophyte of two cells, the lower and larger (wall cell) developing the pollen tube, the upper and smaller (generative cell) giving rise to the sperms.—After SCHIMPER.

male organ. This name should, of course, be abandoned, as the stamen is now known to be a microsporophyll, which is an organ produced by the sporophyte, which never produces sex organs. It should be borne distinctly in mind that the stamen is not a sex organ, for the literature of botany is full of this old assumption, and the beginner is in

danger of becoming confused and of forgetting that pollen grains are asexual spores.

98. **Megasporophylls.**—The strobili composed of megasporophylls become much larger than the others, forming

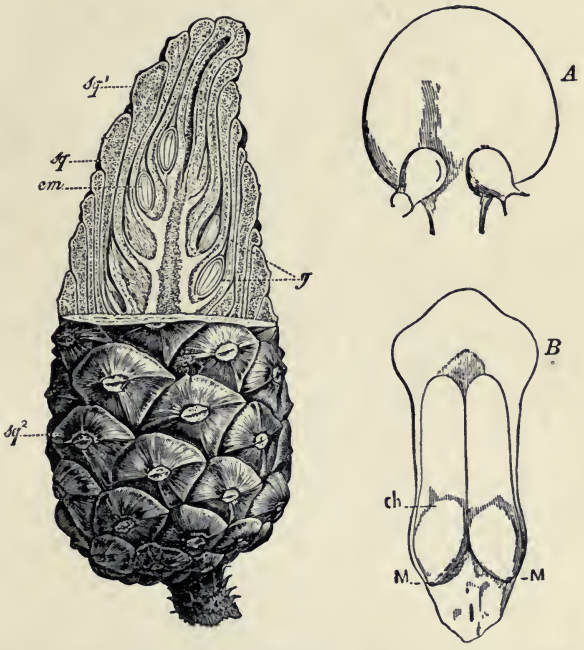


FIG. 147. *Pinus sylvestris*, showing mature cone partly sectioned, and showing carpels (*sq*, *sq*¹, *sq*²) with seeds in their axils (*g*), in which the embryos (*em*) may be distinguished; *A*, a young carpel with two megasporangia; *B*, an old carpel with mature seeds (*ch*), the micropyle being below (*M*).—After BESSEY.

the well-known cones so characteristic of pines and their allies (Figs. 145, *a*, *b*, *c*, 163). Each sporophyll is somewhat leaf-like, and at its base upon the upper side are two megasporangia (Fig. 147). It is these sporangia which are peculiar in each producing and retaining a solitary large megaspore. This megaspore resembles a sac-like cavity in

the body of the sporangium (Fig. 148, *d*), and was at first not recognized as being a spore.

These structures had also received names before they were identified with the corresponding structures of the lower groups. The megasporophyll was called a *carpel*, the megasporangia *ovules*, and the megaspore an *embryo-sac*, because the young embryo was observed to develop within it (Fig. 147, *em*).

The strobilus of megasporophylls, therefore, may be called the *carpellate strobilus* or *carpellate cone*. As the carpel enters into the organization of a structure known as the *pistil*, to be described later, the cone is often called the *pistillate cone*. As the staminate cone is sometimes wrongly called a "male cone," so the carpellate cone is wrongly called a "female cone," the old idea being that the carpel with its ovules represented the female sex organ.

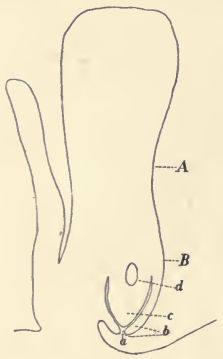


FIG. 148. Diagram of the carpel structures of pine, showing the heavy scale (*A*) which bears the ovule (*B*), in which are seen the micropyle (*a*), integument (*b*), nucellus (*c*), embryo sac or megaspore (*d*).—CALDWELL.

The structure of the megasporangium, or ovule, must be known. The main body is the *nucellus* (Figs. 148, *c*, 149, *nc*); this sends out from near its base an outer membrane (*integument*) which is distinct above (Figs. 148 *b*, 149 *i*), covering the main part of the nucellus and projecting beyond its apex as a prominent neck, the passage through which to the apex of the nucellus is called the *micropyle* ("little gate") (Fig. 148, *a*). Centrally placed within the body of the nucellus is the conspicuous cavity called the embryo-sac (Fig. 148, *d*), in reality the retained megaspore. The relations between integument, micropyle, nucellus, and embryo-sac should be kept clearly in mind. In the

pine the micropyle is directed downward, toward the base of the sporophyll (Figs. 147, 148).

99. **Female gametophyte.**—The female gametophyte is always produced by the germination of a megaspore, and therefore it should be produced by the so-called embryo-sac within the ovule. This imbedded megaspore germinates, just as does the megaspore of *Selaginella* or *Isoetes*, by cell division becoming filled with a compact mass of nutritive tissue representing the ordinary cells of the female prothallium (Fig. 149, *e*). This prothallium naturally does not protrude beyond the boundary of the megaspore wall, being completely surrounded by the tissues of the sporangium. It must be evident that this gametophyte is absolutely dependent upon the sporophyte for its nutrition, and remains not merely attached to it, but is actually imbedded within its tissues like an internal parasite. So conspicuous a tissue within the ovule, as well as in the seed into which the

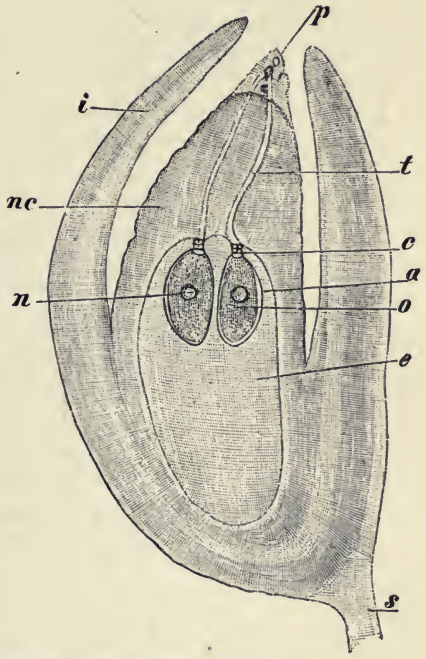


Fig. 149. Diagrammatic section through ovule (megasporangium) of spruce (*Picea*), showing integument (*i*), nucellus (*nc*), endosperm or female gametophyte (*e*) which fills the large megaspore imbedded in the nucellus, two archegonia (*a*) with short neck (*c*) and venter containing the egg (*o*), and position of germinating pollen grains or microspores (*p*) whose tubes (*t*) penetrate the nucellus tissue and reach the archegonia.—After Schimper.

ovule develops, did not escape early attention, and it was called *endosperm,* meaning "within the seed." The endosperm of Gymnosperms, therefore, is the female gametophyte.

At the margin of the endosperm nearest the micropyle regular flask-shaped archegonia are developed (Fig. 149, *a*), making it sure that the endosperm is a female gametophyte. It is evident that the necks of these archegonia (Fig. 149, *c*) are shut away from the approach of sperms by swimming, and that some new method of approach must be developed.

100. **Male gametophyte.**—The microspores are developed in the sporangium in the usual tetrad fashion, and are produced and scattered in very great abundance. It will be remembered that the male gametophyte developed by the microspore of *Selaginella* is contained entirely within the spore, and consists of a single ordinary prothallial cell and one antheridium (see § 89). In the pine it is no better developed. One or two small cells appear, which may be regarded as representing prothallial cells, while the rest of the gametophyte seems to be a single antheridium (Fig. 146, *D*). At first this antheridium seems to consist of a large cell called the *wall cell,* and a small one called the *generative cell.* Sooner or later the generative cell divides and forms two small cells, one of which divides again and forms two cells called *male cells,* which seem to represent the sperm mother cells of lower plants. The three active cells of the completed antheridium, therefore, are the wall cell, with a prominent nucleus, and two small male cells which are free in the large wall cell.

These sperm mother cells (male cells) do not form sperms within them, as there is no water connection between them and the archegonia, and a new method of transfer is provided. This is done by the wall cell, which develops a tube, known as the *pollen-tube.* Into this tube the male cells enter, and as it penetrates among the cells

which shut off the archegonia it carries the male cells along, and so they are brought to the archegonia (Fig. 150).

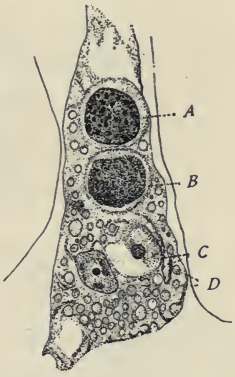


Fig. 150. Tip of pollen tube of pine, showing the two male cells (*A*, *B*), two nuclei (*C*) which accompany them, and the numerous food granules (*D*): the tip of the tube is just about to enter the neck of the archegonium.—Caldwell.

Fig. 151. Pollen tube passing through the neck of an archegonium of spruce (*Picea*), and containing near its tip the two male nuclei, which are to be discharged into the egg whose cytoplasm the tube is just entering.—After Strasburger.

101. **Fertilization.**—Before fertilization can take place the pollen-grains (microspores) must be brought as near as possible to the female gametophyte with its archegonia. The spores are formed in very great abundance, are dry and powdery, and are scattered far and wide by the wind. In the pines and their allies the pollen-grains are winged (Fig. 146, *D*), so that they are well organized for wind distribution. This transfer of pollen is called *pollination*, and those plants that use the wind as an agent of transfer are said to be *anemophilous*, or "wind-loving."

The pollen must reach the ovule, and to insure this it must fall like rain. To aid in catching the falling pollen the scale-like carpels of the cone spread apart, the pollen grains slide down their sloping surfaces and collect in a

little drift at the bottom of each carpel, where the ovules are found (Fig. 147, *A*, *B*). The flaring lips of the micropyle roll inward and outward as they are dry or moist, and by this motion some of the pollen-grains are caught and pressed down upon the apex of the nucellus.

In this position the pollen-tube develops, crowds its way among the cells of the nucellus, reaches the wall of the embryo-sac, and penetrating that, reaches the necks of the archegonia (Fig. 149, *p*, *t*); crowding into them (Fig. 151), the tip of the tube opens, the male cells are

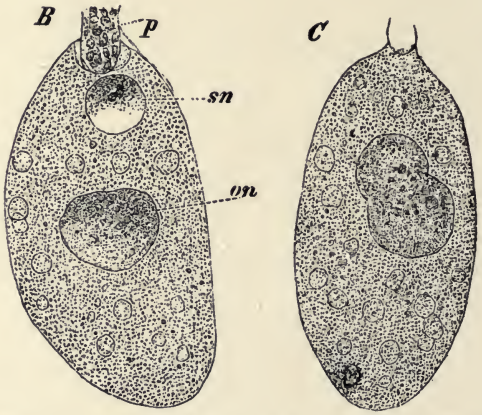


Fig. 152. Fertilization in spruce (*Picea*): *B* is an egg, in the tip of which a pollen tube (*p*) has entered and has discharged into the cytoplasm a male nucleus (*sn*), which is to unite with the egg (female) nucleus (*on*); *C*, a later stage in which the two nuclei are uniting.—After Schimper.

discharged, one male cell fuses with the egg (Fig. 152), and fertilization is accomplished, an oospore being formed in the venter of the archegonium.

It will be noticed that the cell which acts as a male gamete is really the sperm mother cell, which does not organize a sperm in the absence of a water connection. This peculiar method of transferring the male cells by means of a special tube developed by the antheridium is

called *siphonogamy*, which means "sexual reproduction by means of a tube." So important is this character among Spermatophytes that some have proposed to call the group *Siphonogams*.

102. **Development of the embryo.**—The oospore when formed lies at the surface of the endosperm (female gametophyte) nearest to the micropyle. As the endosperm is to supply nourishment to the embryo, this position is not the most favorable. Therefore, as in *Selaginella*, the oospore first develops a suspensor, which in pine and its allies becomes very long and often tortuous (Fig. 153, *A*, *s*). At the tip of the suspensor the cell or cells (embryo cells) which are to develop the embryo are carried (Fig. 153, *A*, *ka*), and thus become deeply buried, about centrally placed, in the endosperm.

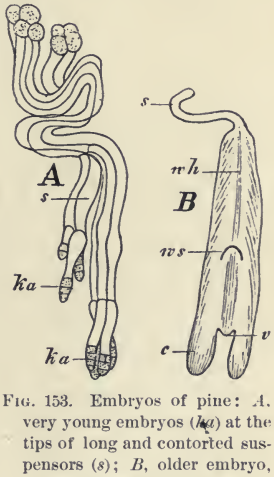


FIG. 153. Embryos of pine: *A*, very young embryos (*ka*) at the tips of long and contorted suspensors (*s*); *B*, older embryo, showing attachment to suspensor (*s*), the extensive root sheath (*wh*), root tip (*ws*), stem tip (*v*), and cotyledons (*c*).—After STRASBURGER.

Several suspensors may start from as many archegonia in the same ovule, and several embryos may begin to develop, but as a rule only one survives, and the solitary completed embryo (Fig. 153, *B*) lies centrally imbedded in the endosperm (Fig. 153*a*). The development of more than one embryo in a megasporangium (ovule) is called *polyembryony*, a phenomenon natural to Gymnosperms with their several archegonia upon a single gametophyte.

103. **The seed.**—While the embryo is developing some important changes are taking place in the ovule outside of the endosperm. The most noteworthy is the change which transforms the integument into a hard bony covering,

known as the *seed coat*, or *testa* (Fig. 153*a*). The development of this testa hermetically seals the structures within, further development and activity are checked, and the living cells pass into the resting condition. This protected structure with its dormant cells is the *seed*.

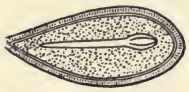


Fig. 153*a*. Pine seed.

In a certain sense the seed is a transformed ovule (megasporangium), but this is true only as to its outer configura-

Fig. 154. Pine seedlings, showing the long hypocotyl and the numerous cotyledons, with the old seed case still attached.—After Atkinson.

tion. If the internal structures be considered it is much more. It is made up of structures belonging to three generations, as follows: (1) The old sporophyte is represented by seed coat and nucellus, (2) the endosperm is a gametophyte, while (3) the embryo is a young sporophyte. It can hardly be said that the seed is simple in structure, or that any real conception of it can be obtained without approaching it by way of the lower groups.

The organization of the seed checks the growth of the embryo, and this development within the seed is known as

FIG. 155. A cycad, showing the palm-like habit, with much branched leaves and scaly stem.—From "Plant Relations."

the *intra-seminal development*. In this condition the embryo may continue for a very long time, and it is a question whether it is death or suspended animation. Is a seed alive? is not an easy question to answer, for it may be kept in a dried-out condition for years, and then when placed in suitable conditions awaken and put forth a living plant.

FIG. 156. *Cycas revoluta*, showing the foliage at the summit of the stem. In the center is the nearly erect cluster of young foliage leaves, below are the scale leaves which covered them in bud, and below these are the widely spreading old foliage leaves.—CALDWELL.

This "awakening" of the seed is spoken of as its "germination," but this must not be confused with the germination of a spore, which is real germination. In the case of the seed an oospore has germinated and formed an embryo, which stops growing for a time, and then resumes it. This resumption of growth is not germination, but is what

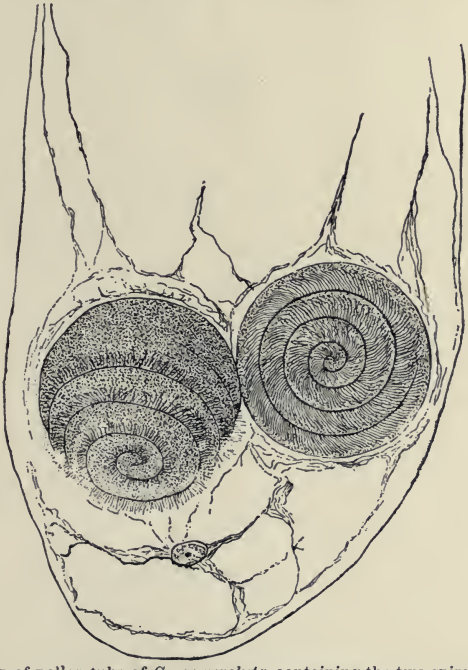


Fig. 157. Tip of pollen tube of *Cycas revoluta*, containing the two spiral, multiciliate sperms.—After Ikeno

happens when a seed is said to "germinate." This second period of development is known as the *extra-seminal*, for it is inaugurated by the escape of the sporophyte from the seed (Fig. 154).

104. **The great groups of Gymnosperms.**—There are at least four living groups of Gymnosperms, and two or three

FIG. 158. A pine (*Pinus*) showing the central shaft and also the bunching of the needle leaves toward the tips of the branches.—From "Plant Relations."

extinct ones. The groups differ so widely from one another in habit as to show that Gymnosperms can be very much diversified. They are all woody forms, but they may be trailing or straggling shrubs, gigantic trees, or high-climbing vines; and their leaves may be needle-like, broad, or "fern-like." For our purpose it will be only necessary to define the two most prominent groups.

105. **Cycads.** — Cycads are tropical, fern-like forms, with large branched (compound) leaves. The stem is either a columnar shaft crowned with a rosette of great branching leaves, with the general habit of tree-ferns and palms (Figs. 155, 156); or they are like great tubers, crowned in the same way. In ancient times (the Mesozoic) they were very abundant, forming a conspicuous feature of the vegetation, but now they are represented only by about eighty forms scattered through both the oriental and occidental tropics.

They are very fern-like in structure as well

FIG. 159. The giant redwood (*Sequoia gigantea*) of California: the relative size is indicated by the figure of a man standing at the right.—After WILLIAMSON.

as in appearance, but they produce seeds and must be associated with Spermatophytes, and as the seed is exposed they are Gymnosperms. A discovery has been made recently that strikingly emphasizes their fern-like structure. In fertilization a pollen-tube develops, as described for pine and its allies, but the male cells (sperm mother - cells) which it contains organize sperms, and these sperms are of the coiled multiciliate type (Fig. 157) characteristic of all the Pteridophytes except Club-mosses. This association of the old ciliated sperm habit with the new pollen-tube habit is a very interesting intermediate or transition condition. It should be said that these sperms have been actually found in but two species of the Cycads, but there are reasons for supposing that they may be found in all. Another one of the Gymnosperm groups, represented today only by the commonly cultivated maid-

FIG. 160. An araucarian pine (*Araucaria*), showing the central shaft, and the regular cycles of branches spreading in every direction and bearing numerous small leaves.—From "Plant Relations."

enhair tree (*Gingko*), with broad dichotomously veined leaves, also develops multiciliate sperms.

The testa of the seed, instead of being entirely hard as described for pine and its allies, develops in two layers, the inner hard and bony, and the outer pulpy, making the ripe fruit resemble a plum.

106. **Conifers.**—This is the great modern Gymnosperm group, and is characteristic of the temperate regions, where it forms great forests. Some of the forms are widely distributed, as the great genus of pines (*Pinus*) (Fig. 158), while some are now very much restricted, although formerly very widely distributed, as the gigantic redwoods (*Sequoia*) of the Pacific slope (Fig. 159). The habit of the body is quite characteristic, a central shaft extending continuously to the very top, while the lateral branches spread horizontally, with diminishing length to the top, forming a conical outline (Figs. 160, 162). This habit of firs, pines, etc., gives them an appearance very distinct from that of other trees.

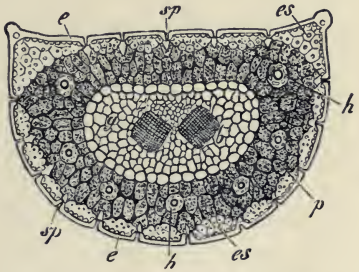


FIG. 161.—Cross-section of a needle-leaf of pine, showing epidermis (*e*) in which there are sunken stomata (*sp*), heavy-walled hypodermal tissue (*es*) which gives rigidity, the mesophyll region (*p*) in which a few resin-ducts (*h*) are seen, and the central region (*stele*) in which two vascular bundles are developed.—After SACHS.

Another peculiar feature is furnished by the characteristic "needle-leaves," which seem to be poorly adapted for foliage. These leaves have small spread of surface and very heavy protecting walls, and show adaptation for enduring hard conditions (Fig. 161). As they have no regular period of falling, the trees are always clothed with them, and have been called "evergreens." There are some notable exceptions to this, however, as in

FIG. 162. A larch (*Larix*), showing the continuous central shaft and horizontal branches, the general outline being distinctly conical. The larch is peculiar among Conifers in periodically shedding its leaves.—From "Plant Relations."

the case of the common larch or tamarack, which sheds its leaves every season (Fig. 162). There are Conifers, also, which do not produce needle-leaves, as in the common arbor-vitæ, whose leaves consist of small closely-overlapping scale-like bodies (Fig. 163).

The two types of leaf arrangement may also be noted. In most Conifers the leaves are arranged along the stem in spiral fashion, no two leaves being at the same level. This is known as the *spiral* or *alternate* arrangement. In other forms, as the cypresses, the leaves are in cycles, as was mentioned in connection with the Horsetails, the arrangement being known as the *cyclic* or *whorled*.

Fig. 163. Arbor-vitæ (*Thuja*), showing a branch with scaly overlapping leaves, and some carpellate cones (strobili).—After Eichler.

The character which gives name to the group is the "cone"—that is, the prominent carpellate cone which becomes so conspicuous in connection with the ripening of the seeds. These cones generally ripen dry and hard (Figs. 145, 147, 163), but sometimes, as in junipers, they become pulpy (Fig. 164), the whole cone forming the so-called "berry."

There are two great groups of Conifers. One, represented by the pines, has true cones which conceal the

ovules, and the seeds ripen dry. The other, represented by the yews, has exposed ovules, and the seed either ripens fleshy or has a fleshy investment.

FIG. 164. The common juniper (*Juniperus communis*); the branch to the left bearing staminate strobili; that to the right bearing staminate strobili above and carpellate strobili below, which latter have matured into the fleshy, berry-like fruit. —After BERG and SCHMIDT.

CHAPTER XII

SPERMATOPHYTES: ANGIOSPERMS

107. **Summary of Gymnosperms.**—Before beginning Angiosperms it is well to state clearly the characters of Gymnosperms which have set them apart as a distinct group of Spermatophytes, and which serve to contrast them with Angiosperms.

(1) The microspore (pollen-grain) by wind-pollination is brought into contact with the megasporangium (ovule), and there develops the pollen-tube, which penetrates the nucellus. This contact between pollen and ovule implies an exposed or naked ovule and hence seed, and therefore the name "Gymnosperm."

(2) The female gametophyte (endosperm) is well organized before fertilization.

(3) The female gametophyte produces archegonia.

108. **General characters of Angiosperms.**—This is the greatest group of plants, both in numbers and importance, being estimated to contain about 100,000 species, and forming the most conspicuous part of the vegetation of the earth. It is essentially a modern group, replacing the Gymnosperms which were formerly the dominant Seed-plants, and in the variety of their display exceeding all other groups. The name of the group is suggested by the fact that the seeds are inclosed in a seed case, in contrast with the exposed seeds of the Gymnosperms.

These are also the true flowering plants, and the appearance of true flowers means the development of an

elaborate symbiotic relation between flowers and insects, through which pollination is secured. In Angiosperms, therefore, the wind is abandoned as an agent of pollen transfer and insects are used; and in passing from Gymnosperms to Angiosperms one passes from anemophilous to *entomophilous* ("insect-loving") plants. This does not mean that all Angiosperms are entomophilous, for some are still wind-pollinated, but that the group is prevailingly entomophilous. This fact, more than anything else, has resulted in a vast variety in the structure of flowers, so characteristic of the group.

109. **The plant body.**—This of course is a sporophyte, the gametophytes being minute and concealed, as in Gymnosperms. The sporophyte represents the greatest possible variety in habit, size, and duration, from minute floating forms to gigantic trees; herbs, shrubs, trees; erect, prostrate, climbing; aquatic, terrestrial, epiphytic; from a few days to centuries in duration.

Roots, stems, and leaves are more elaborate and variously organized for work than in other groups, and the whole structure represents the highest organization the plant body has attained. As in the Gymnosperms, the leaf is the most variously used organ, showing at least four distinct modifications: (1) foliage leaves, (2) scales, (3) sporophylls, and (4) floral leaves. The first three are present in Gymnosperms, and even in Pteridophytes, but floral leaves are peculiar to Angiosperms, making the true flower, and being associated with entomophily.

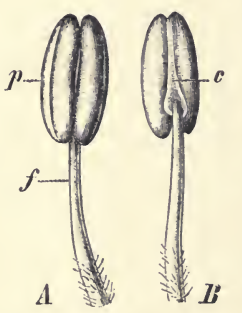


FIG. 165. Stamens of henbane (*Hyoscyamus*): *A*, front view, showing filament (*f*) and anther (*p*); *B*, back view, showing the connective (*c*) between the pollen-sacs. —After SCHIMPER.

110. **Microsporophylls.**—The microsporophyll of Angiosperms is more definitely known as a "stamen" than

that of Gymnosperms, and has lost any semblance to a leaf. It consists of a stalk-like portion, the *filament;* and a sporangia-bearing portion, the *anther* (Figs. 165, 167*a*).

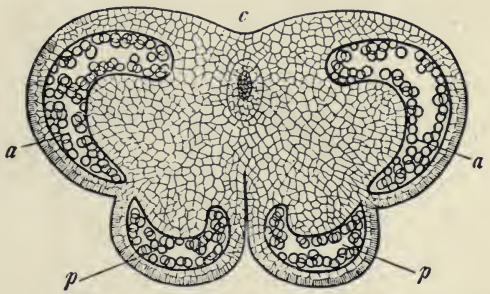


Fig. 166. Cross-section of anther of thorn apple (*Datura*), showing the four imbedded sporangia (*a*, *p*) containing microspores; the pair on each side will merge and dehisce along the depression between them for the discharge of pollen.—After Frank.

The filament may be long or short, slender or broad, or variously modified, or even wanting. The anther is simply the region of the sporophyll which bears sporangia, and is

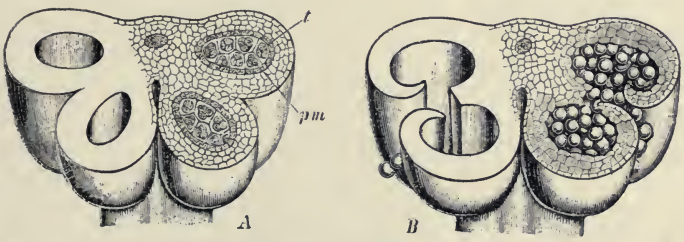


Fig. 167. Diagrammatic cross sections of anthers: *A*, younger stage, showing the four imbedded sporangia, the contents of two removed, but the other two containing pollen mother cells (*pm*) surrounded by the tapetum (*t*); *B*, an older stage, in which the microspores (pollen grains) are mature, and the pair of sporangia on each side are merging together to form a single pollen-sac with longitudinal dehiscence.—After Baillon and Luerssen.

therefore a composite of sporophyll and sporangia and is often of uncertain limitation. Such a term is convenient, but is not exact or scientific.

If a young anther be sectioned transversely four sporangia will be found imbedded beneath the epidermis, a pair on each side of the axis (Figs. 166, 167). When they reach maturity, the paired sporangia on each side usually merge together, forming two spore-containing cavities (Fig. 167, *B*). These are generally called "pollen-sacs," and each anther is said to consist of two pollen-sacs, although each sac is made up of two merged sporangia, and is not the equivalent of the pollen-sac in Gymnosperms, which is a single sporangium.

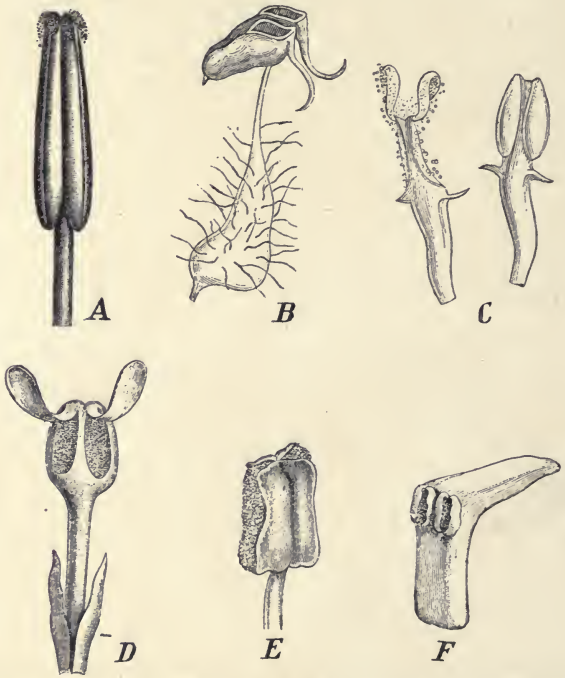


FIG. 167*a*. Various forms of stamens: *A*, from *Solanum*, showing dehiscence by terminal pores; *B*, from *Arbutus*, showing anthers with terminal pores and "horns"; *C*, from *Berberis*; *D*, from *Atherosperma*, showing dehiscence by uplifted valves; *E*, from *Aquilegia*, showing longitudinal dehiscence; *F*, from *Popowia*, showing pollen-sacs near the middle of the stamen.—After ENGLER and PRANTL.

The opening of the pollen-sac to discharge its pollen-grains (microspores) is called *dehiscence*, which means "a splitting open," and the methods of dehiscence are various (Fig. 167*a*). By far the most common method is for the wall of each sac to split lengthwise (Fig. 168), which is called *longitudinal dehiscence;* another is for each sac to open by a terminal pore (Fig. 167*a*), in which case it may be prolonged above into a tube.

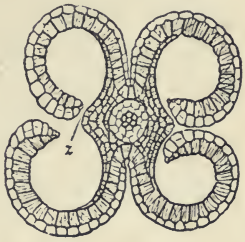


Fig. 168. Cross-section of anther of a lily (*Butomus*), showing the separating walls between the members of each pair of sporangia broken down at *z*, forming a continuous cavity (pollen sac) which opens by a longitudinal slit.—After Sachs.

111. **Megasporophylls.** — These are the so-called "carpels" of Seed-plants, and in Angiosperms they are organized in various ways, but always so as to inclose the mega-sporangia (ovules). In the simplest cases each carpel is independent (Fig. 169, *A*), and is differentiated into three regions: (1) a hollow bulbous base, which contains the ovules and is the real seed case, known as the *ovary;* (2) surmounting this is a slender more or less elongated process, the *style;* and (3) usually at or near the apex of the style a special receptive surface for the pollen, the *stigma*.

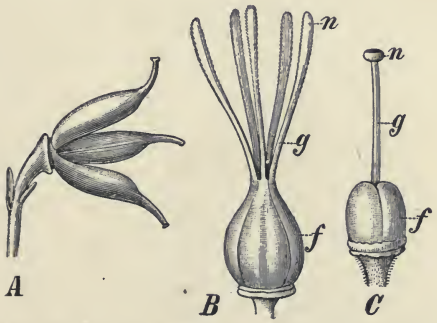


Fig. 169. Types of pistils: *A*, three simple pistils (apocarpous), each showing ovary and style tipped with stigma; *B*, a compound pistil (syncarpous), showing ovary (*f*), separate styles (*g*), and stigmas (*n*); *C*, a compound pistil (syncarpous), showing ovary (*f*), single style (*g*), and stigma (*n*).—After Berg and Schmidt.

In other cases several carpels to-

gether form a common ovary, while the styles may also combine to form one style (Fig. 169, *C*), or they may remain more or less distinct (Fig. 169, *B*). Such an ovary may contain a single chamber, as if the carpels had united edge to edge (Fig. 170, *A*); or it may contain as many chambers as there are constituent carpels (Fig. 170, *B*), as though each carpel had formed its own ovary before coalescence. In ordinary phrase an ovary is either "one-celled" or "several-celled," but as the word "cell" has a very different application, the ovary chamber had better be called a *loculus*, meaning "a compartment." Ovaries,

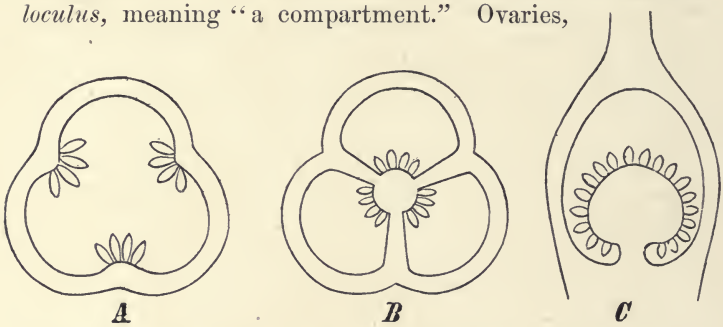


FIG. 170. Diagrammatic sections of ovaries: *A*, cross-section of an ovary with one loculus and three carpels, the three sets of ovules said to be attached to the wall (parietal); *B*, cross-section of an ovary with three loculi and three carpels, the ovules being in the center (central); *C*, longitudinal section of *B*.—After SCHIMPER.

therefore, may have one loculus or several loculi. Where there are several loculi each one usually represents a constituent carpel (Fig. 170, *B*); where there is one loculus the ovary may comprise one carpel (Fig. 169, *A*), or several (Fig. 170, *A*).

There is a very convenient but not a scientific word, which stands for any organization of the ovary and the accompanying parts, and that is *pistil*. A pistil may be one carpel (Fig. 169, *A*), or it may be several carpels organized together (Fig. 169, *B*, *C*), the former case being a *simple pistil*, the latter a *compound pistil*. In other words,

any organization of carpels which appears as a single organ with one ovary is a pistil.

The ovules (megasporangia) are developed within the ovary (Fig. 170) either from the carpel wall, when they are foliar, or from the stem axis which ends within the ovary, when they are cauline (see § 89). They are similar in structure to those of Gymnosperms, with integument and micropyle, nucellus, and embryo-sac (megaspore), except that there are often two integuments, an outer and an inner (Fig. 171).

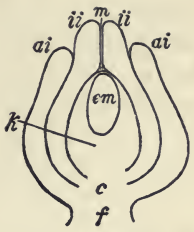


Fig. 171. A diagrammatic section of an ovule of Angiosperms, showing outer integument (*ai*), inner integument (*ii*), micropyle (*m*), nucellus (*k*), and embryo sac or megaspore (*em*).—After Sachs.

112. **The male gametophyte.** — When the pollen-grain (microspore) germinates there is formed within it the simplest known gametophyte (Fig. 172). No trace of the

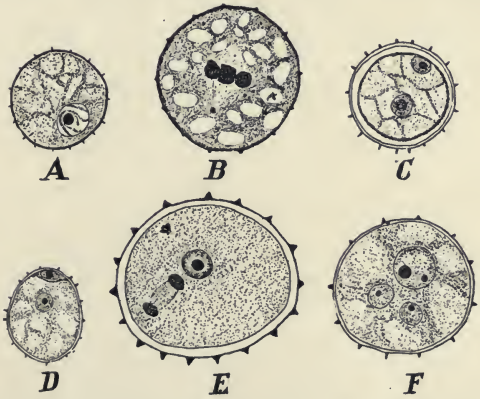


Fig. 172. Germination of microspore (pollen grain) in duckweed (*Lemna*): *A*, mature spore with its nucleus; *B*, nucleus of spore dividing; *C*, two nuclei resulting from the division; *D*, a large and small cell following the nuclear division, forming the two-celled male gametophyte; *E*, division of smaller cell (generative) to form the two male cells; *F*, the two male cells completed and lying near the large tube nucleus.—Caldwell.

ordinary nutritive cells of the gametophyte remains, and the whole structure seems to represent a single antheridium. At first it consists of two cells, the large wall cell and the small free generative cell (Fig. 172, *D*). Later the generative cell divides (Fig. 172, *E*), either while in the pollen-grain or after entrance into the pollen-tube, and two male cells (sperm mother-cells) are formed (Fig. 172, *F*), which do not organize sperms, but which function directly as gametes.

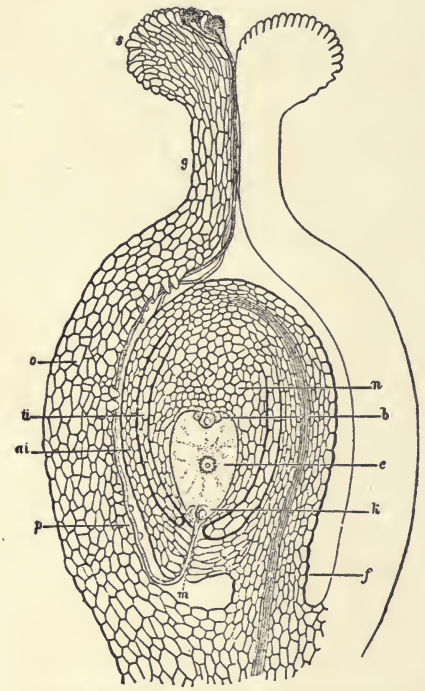


FIG. 173. Diagram of a longitudinal section through a carpel, to illustrate fertilization with all parts in place: *s*, stigma; *g*, style; *o*, ovary; *ai*, *ii*, outer and inner integuments; *n*, base of nucellus; *f*, funiculus; *b*, antipodal cells; *c*, endosperm nucleus; *k*, egg and one synergid; *p*, pollen-tube, having grown from stigma and passed through the micropyle (*m*) to the egg.—After LUERSSEN.

When pollination occurs, and the pollen has been transferred from the pollen-sacs to the stigma, it is detained by the minute papillæ of the stigmatic surface, which also excretes a sweetish sticky fluid. This fluid is a nutrient solution for the microspores, which begin to put out their tubes. A pollen-tube penetrates through the stigmatic surface, enters among the tissues of the style, which is sometimes very long, slowly or rapidly traverses the length of the style supplied with food by

its cells but not penetrating them, enters the cavity of the ovary, passes through the micropyle of an ovule, penetrates the tissues of the nucellus (if any), and finally reaches and pierces the wall of the embryo-sac, within which is the egg awaiting fertilization (Fig. 173).

This remarkable ability of the pollen-tube to make its way through so much tissue, directly to the micropyle of an inclosed ovule, can only be explained by supposing that it is under the guidance of some strong attraction.

113. **The female gametophyte.**—The megaspore (embryo-sac) occupies the same position in the ovule as in Gymnosperms, but its germination is remarkably modified. The development of the female gametophyte shows two distinct

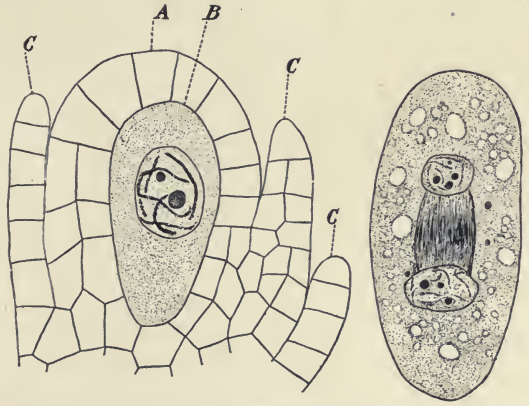


FIG. 174. *Lilium Philadelphicum:* to the left a young megasporangium (ovule), showing integuments (*C*), nucellus (*A*), and megaspore (*B*) containing a large nucleus. To the right a megaspore whose nucleus is undergoing the first division in the formation of the gametophyte.—CALDWELL.

periods, separated from one another by the act of fertilization. If fertilization is not accomplished the second stage of the gametophyte is usually not developed.

First period.—The megaspore nucleus divides (Fig. 174), and one nucleus passes to each end of the embryo-

sac (Fig. 175, at left). Each of these nuclei divide (Fig. 175, at right), and two nuclei appear at each end of the sac (Fig. 175, at middle). Each of the four nuclei divide

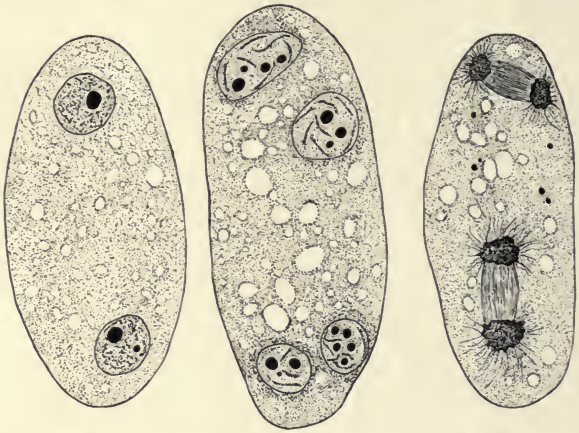


FIG. 175. *Lilium Philadelphicum:* to the left is an embryo-sac with a gametophyte nucleus in each end; to the right these two nuclei are dividing to form the two nuclei shown in each end of the sac in the middle figure.—CALDWELL.

(Fig. 176, at left), and four nuclei appear at each end (Fig. 176, at middle). When eight nuclei have appeared, nuclear division stops. Then a remarkable phenomenon occurs. One nucleus from each end, the two being called "polar nuclei," moves toward the center of the sac, the two meet and fuse (Fig. 176, at right, *C*), and a single large nucleus is the result.

The three nuclei at the end of the sac nearest the micropyle are organized into cells, each being definitely surrounded by cytoplasm, but there is no wall and the cells remain naked but distinct. These three cells constitute the *egg-apparatus* (Fig. 176, at right, *A*), the central one, which usually hangs lower in the sac than the others, being the egg, the two others being the *synergids*, or "helpers." Here, therefore, is an egg without an archegonium, a distinguishing feature of Angiosperms.

The three nuclei at the other end of the sac are also organized into cells, and usually have walls. These cells are known as *antipodal cells* (Fig. 176, at right, *B*). The large nucleus near the center of the sac, formed by the fusion of the two

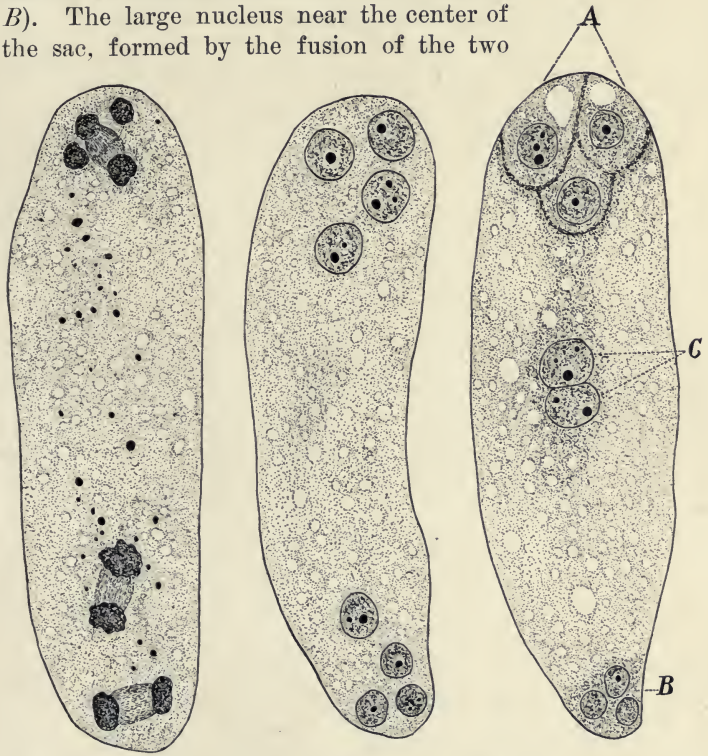


FIG. 176. *Lilium Philadelphicum*, showing last stages of germination of megaspore before fertilization: the embryo sac to the left contains the pair of nuclei in each end in a state of division preparatory to the stage represented by the middle figure, in which there are four nuclei at each end; the figure to the right shows an embryo-sac containing a gametophyte about ready for fertilization, with the egg apparatus (*A*) composed of the two synergids and egg (central and lower), the three antipodal cells (*B*), and the two polar nuclei fusing (*C*) to form the primary endosperm nucleus.—CALDWELL.

polar nuclei, is known as the *primary endosperm nucleus* or the *definitive nucleus*.

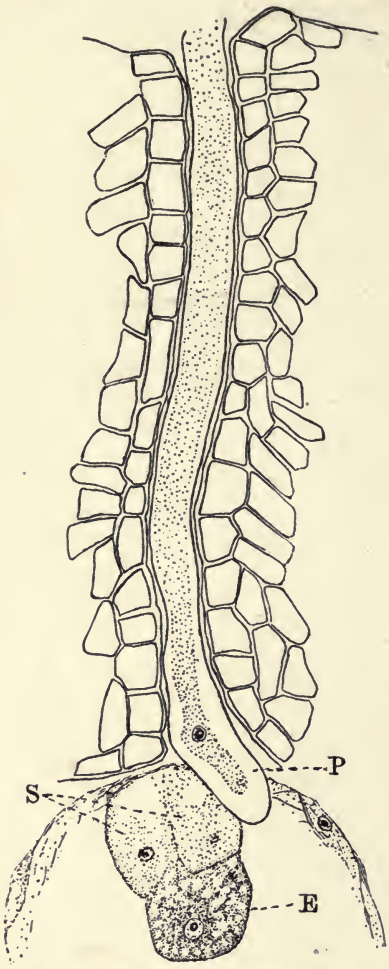


FIG. 177. Fertilization in the cotton plant, a Dicotyledon, showing the pollen tube (*P*) passing through the micropyle and containing a single sperm (male cell), and having entered the embryo-sac is in contact with one of the synergids (*S*) on its way to the egg (*E*).—After DUGGAR.

This completes the first period of gametophyte development, and it is ready for fertilization.

Fertilization. — The pollen-tube, carrying the two male cells, has passed down the style and entered the micropyle (Fig. 173). It then reaches the wall of the embryo-sac, pierces it, and is in contact with the egg-apparatus. Usually it passes along the side of one of the synergids (Fig. 177), feeding upon and disorganizing it. When it comes near the conspicuous nucleus of the egg, the tip of the tube breaks and one male cell is discharged into the cytoplasm of the egg (Fig. 178). The egg and the male cell now fuse, and an oospore, which invests itself with a wall, is the result.

Second period.—After fertilization the gametophyte begins its second period of development. The primary endosperm nucleus begins a series of divisions, and as a result

the sac becomes more or less filled with nutritive cells, which are often organized into a compact tissue (Fig. 179). These nutritive cells correspond to the endosperm of Gymnosperms, and receive the same name. In Gymnosperms, therefore, the endosperm (the nutritive body of the female gametophyte) is mainly formed before fertilization, while in Angiosperms it is mainly formed after fertilization. This means that in Angiosperms eggs are formed and fertilization takes place in a very young gametophyte, while in Gymnosperms and heterosporous Pteridophytes the eggs appear much later.

The antipodal cells also probably represent nutritive cells of the gametophyte. Sometimes they dis-

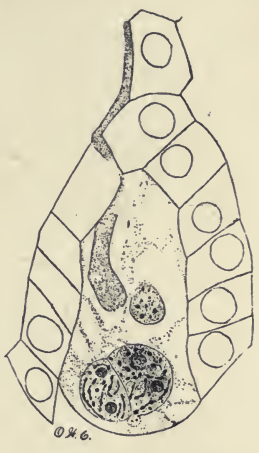


FIG. 178. End of embryo-sac of lily (*Lilium Philadelphicum*): a pollen tube has entered the sac and has discharged a male cell, whose nucleus is seen uniting with the nucleus of the egg; near the tip of the tube is the disorganizing nucleus of one of the synergids. —CALDWELL.

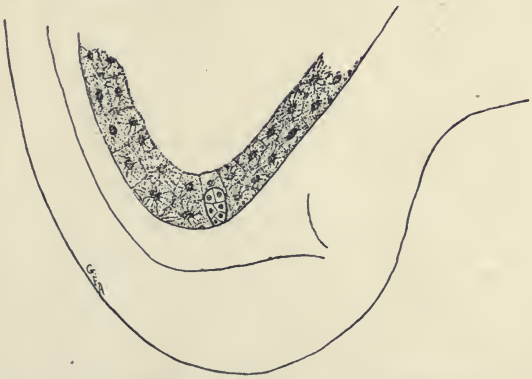


FIG. 179. One end of the embryo-sac in wake-robin (*Trillium*), showing endosperm (shaded cells) in which a young embryo is imbedded.—After ATKINSON.

appear very soon after they are formed; but sometimes they become very active and even divide and form a considerable amount of tissue, aiding the endosperm in nourishing the young embryo.

114. **Development of embryo.**—While the endosperm is forming, the oospore has germinated and the sporophyte embryo is developing (Fig. 180). Usually a suspensor, more or less distinct, but never so prominent as in Gymnosperms, is formed; at the end of it the embryo is developed (Fig. 181), which, when completed, is more or less surrounded by nourishing endosperm (Fig. 183).

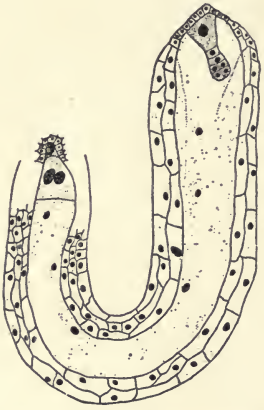


FIG. 180. Curved embryo-sac of arrowhead (*Sagittaria*), showing in the upper right end a young embryo, in the other end the antipodal cells cut off by a partition, and scattered through the sac a few free endosperm cells.—After SCHAFFNER.

The two groups of Angiosperms differ widely in the structure of the embryo. In Monocotyledons the axis of the embryo develops the root-tip at one end and the "seed-leaf" (cotyledon) at the other, the stem-tip arising from the side of the axis as a lateral member (Fig. 182). This relation of organs recalls the embryo of *Isoetes* (see § 90). Naturally there can be but one cotyledon under such circumstances, and the group has been named *Monocotyledons*.

In Dicotyledons the axis of the embryo develops the root-tip at one end and the stem-tip at the other, the cotyledons (usually two) appearing as a pair of opposite lateral members on either side of the stem-tip (Fig. 181). This recalls the relation of parts in the embryo of *Selaginella* (see § 89). As the cotyledons are lateral members their number may vary. In Gymnosperms, whose embryos are of this type, there are often

several cotyledons in a cycle (Fig. 154); and in Dicotyledons there may be one or three cotyledons; but as a pair of opposite cotyledons is almost without exception in the group, it is named *Dicotyledons*.

The axis of the embryo between the root-tip and the cotyledons is called the *hypocotyl* (Figs. 154, 193, 194), which

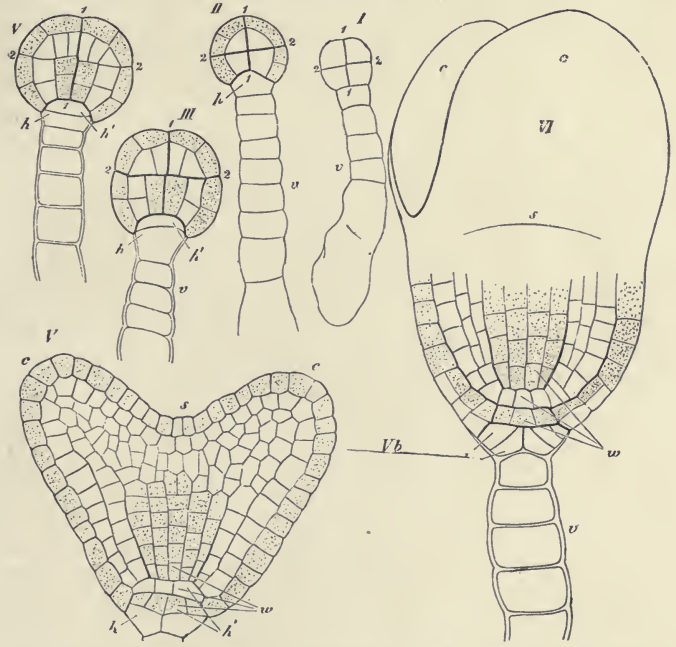


Fig. 181. Development of embryo of shepherd's purse (*Capsella*), a Dicotyledon: beginning with *I*, the youngest stage, and following the sequence to *VI*, the oldest stage, *v* represents the suspensor, *c* the cotyledons, *s* the stem-tip, *w* the root, *h* the root-cap. Note the root-tip at one end of the axis and the stem-tip at the other between the cotyledons.—After Hanstein.

means "under the cotyledon," a region which shows peculiar activity in connection with the escape of the embryo from the seed. Formerly it was called either *caulicle* or *radicle*. In Dicotyledons the stem-tip between the coty-

ledons often organizes the rudiments of subsequent leaves, forming a little bud which is called the *plumule*.

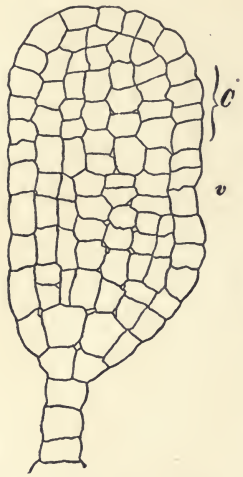


FIG. 182. Young embryo of water plantain (*Alisma*), a Monocotyledon, the root being organized at one end (next the suspensor), the single cotyledon (*C*) at the other, and the stem-tip arising from a lateral notch (*v*). — After HANSTEIN.

Embryos differ much as to completeness of their development within the seed. In some plants, especially those which are parasitic or saprophytic, the embryo is merely a small mass of cells, without any organization of root, stem, or leaf. In many cases the embryo becomes highly developed, the endosperm being used up and the cotyledons stuffed with food material, the plumule containing several well-organized young leaves, and the embryo completely filling the seed cavity. The common bean is a good illustration of this last case, the whole seed within the integument consisting of the two large, fleshy cotyledons, between which lie the hypocotyl and a plumule of several leaves.

115. **The seed.** — As in Gymnosperms, while the processes above described are taking place within the ovule, the integument or integuments are becoming transformed into the testa (Fig. 183). When this hard coat is fully developed, the activities within cease, and the whole structure passes into that condition of suspended animation which is so little understood, and which may continue for a long time.

The testa is variously developed in seeds, sometimes being smooth and glistening, sometimes pitted, sometimes rough with warts or ridges. Sometimes prominent appendages are produced which assist in seed-dispersal, as the wings in *Catalpa* or *Bignonia* (Fig. 184), or the tufts of

FIG. 183. The two figures to the left are seeds of violet, one showing the black, hard testa, the other being sectioned and showing testa, endosperm, and imbedded embryo; the figure to the right is a section of a pepper fruit (*Piper*), showing modified ovary wall (*pc*), seed testa (*sc*), nucellus tissue (*p*), endosperm (*en*), and embryo (*em*).—After ATKINSON.

hair on the seeds of milkweed, cotton, or fireweed (Fig. 185). For a fuller account of the methods of seed-dispersal see *Plant Relations,* Chapter VI.

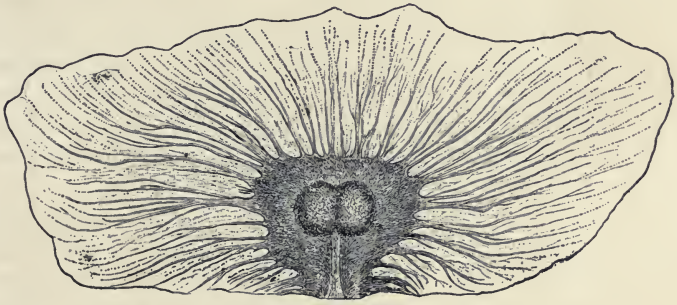


FIG. 184. A winged seed of *Bignonia.*—After STRASBURGER.

116. **The fruit.**—The effect of fertilization is felt beyond the boundaries of the ovule, which forms the seed. The ovary is also involved, and becomes more or less modified. It enlarges more or less, sometimes becoming remarkably enlarged. It also changes in structure, often becoming hard or parchment-like. In case it contains several or numerous seeds, it is organized to open in some way and discharge them, as in the ordinary *pods* and *capsules* (Fig. 185). In case there is but one seed, the modified ovary

FIG. 185. A pod of fireweed (*Epilobium*) opening and exposing its plumed seeds which are transported by the wind.—After BEAL.

wall may invest it as closely as another integument, and a seed-like fruit is the result—a fruit which never opens and is practically a seed. Such a fruit is known as an *akene*, and is very characteristic of the greatest Angiosperm family, the Compositæ, to which sunflowers, asters, golden-rods, daisies, thistles, dandelions, etc., belong. Dry fruits which do not open to discharge the seed often bear appendages to aid in dispersal by wind (Figs. 186, 187), or by animals (Fig. 188).

Capsules, pods, and akenes are said to be dry fruits, but in many cases fruits ripen fleshy. In the peach, plum, cherry, and all ordinary "stone fruits," the modified ovary wall organizes two layers, the inner being very hard, forming the "stone," the outer being pulpy (Fig. 189), or variously modified (Fig. 190). In the true berries, as the grape, currant, tomato, etc., the whole ovary becomes a thin-skinned pulpy mass in which the seeds are imbedded.

In some cases the effect of fertilization in changing structure is felt beyond the ovary. In the apple, pear, quince, and such fruits, the pulpy part is the modified calyx (one of the

FIG. 186. Winged fruit of maple.—After KERNER.

floral leaves), the ovary and its contained seeds being represented by the "core." In other cases, the end of the stem bearing the ovaries (receptacle) becomes enlarged and pulpy, as in the strawberry (Fig. 191). This effect sometimes involves even more than the parts of a single flower, a whole flower-cluster, with its axis and bracts, becoming an enlarged pulpy mass, as in the pineapple (Fig. 192).

The term "fruit," therefore,

FIG. 187. A ripe dandelion head, showing the mass of plumes, a few seed-like fruits (akenes) with their plumes still attached to the receptacle, and two fallen off.—After KERNER.

FIG. 188. An akene of beggar ticks, showing the two barbed appendages which lay hold of animals.—After BEAL.

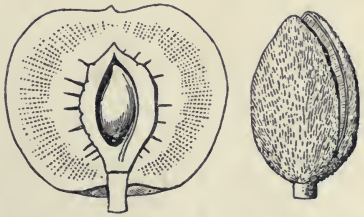


FIG. 189. To the left a section of a peach (fruit), showing pulp and stone formed from ovary wall, and the contained seed (kernel); to the right the fruit of almond, which ripens dry.—After GRAY.

is a very indefinite one, so far as the structures it includes are concerned. It is simply an effect which follows fertilization, and involves more or less of the structures adja-

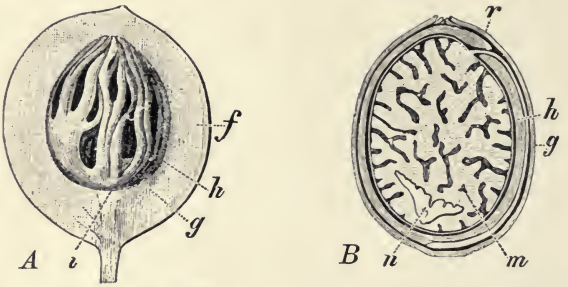


FIG. 190. Fruit of nutmeg (*Myristica*): *A*, section of fruit, showing seed within the heavy wall; *B*, section of seed, showing peculiar convoluted and hard endosperm (*m*) in which an embryo (*n*) is imbedded —After BERG and SCHMIDT.

cent to the seeds. As has been seen, this effect may extend only to the ovary wall, or it may include the calyx, or it may be specially directed toward the receptacle, or it may embrace a whole flower-cluster. It is what is called a physiological effect rather than a definite morphological structure.

FIG. 191. Fruit of strawberry, showing the persistent calyx, and the enlarged pulpy receptacle in which numerous simple and dry fruits (akenes) are imbedded.—After BAILEY.

117. **Germination of the seed.**—It has been pointed out (§ 103) that the so-called "germination of the seed" is not true germination like that of spores. It is the awakening and escape of the young sporophyte, which has long before passed through its germination stage.

By various devices seeds are separated from the parent plant, are dispersed more or less widely, and find lodgment. If the lodgment is suitable, there are many devices for burial, such as twisting stalks and awns, bur-

rowing animals, etc. The period of rest may be long or short, but sooner or later, under the influence of moisture, suitable temperature, and oxygen the quiescent seed begins to show signs of life.

The sporophyte within begins to grow, and the seed coat is broken or penetrated through some thin spot or

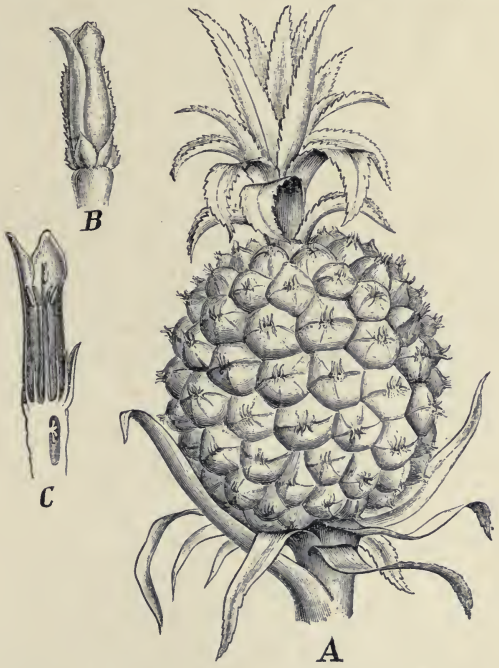


FIG. 192. Pineapple: *A*, the cluster of fruits forming the so-called "fruit"; *B*, single flower, showing small calyx and more prominent corolla; *C*, section of flower, showing the floral organs arising above the ovary (epigynous).—*A*, *B* after KOCH; *C* after LE MAOUT and DECAISNE.

opening. The root-tip emerges first, is protruded still farther by the rapid elongation of the hypocotyl, soon curves toward the earth, penetrates the soil, and sending out rootlets, becomes anchored. After anchorage in the

soil, the hypocotyl again rapidly elongates and develops a strong arch, one of whose limbs is anchored, and the other is pulling upon the cotyledons (Fig. 193). This pull finally frees the cotyledons, the hypocotyl straightens, the cotyle-

FIG. 193. Germination of the garden bean, showing the arch of the hypocotyl above ground, its pull on the seed to extricate the cotyledons and plumule, and the final straightening of the stem and expansion of the young leaves.—After ATKINSON.

dons are spread out to the air and light, and the young sporophyte has become independent (Fig. 194).

In the grain of corn and other cereals, so often used in the laboratory as typical Monocotyledons, but really exceptional ones, the embryo escapes easily, as it is placed on one side of the seed near the surface. The hypocotyl and stem split the thin covering, and the much-modified cotyledon is left within the grain to absorb nourishment.

In some cases the cotyledons do not escape from the seed, either being distorted with food storage (oak, buckeye, etc.), or being retained to absorb nourishment from the endosperm (palms, grasses, etc.). In such cases the stem-tip is liberated by the elongation of the petioles of the

cotyledons, and the seed coat containing the cotyledons remains like a lateral appendage upon the straightened axis.

It is also to be observed in many cases that the young root system, after gripping the soil, contracts, drawing the young plant deeper into the ground.

118. **Summary from Angiosperms.**—At the beginning of this chapter (§ 107) the characters of the Gymnosperms were summarized which distinguished them from Angiosperms, whose contrasting characters may be stated as follows:

(1) The microspore (pollen-grain), chiefly by insect pollination, is brought into contact with the stigma, which is a receptive region on the surface of the carpel, and there develops the pollen-tube, which penetrates the style to reach the ovary cavity which contains the ovules (megasporangia). The impossibility of contact between pollen and ovule implies inclosed ovules and hence seeds, and therefore the name "Angiosperm."

(2) The female gametophyte is but slightly developed before fertilization, the egg appearing very early.

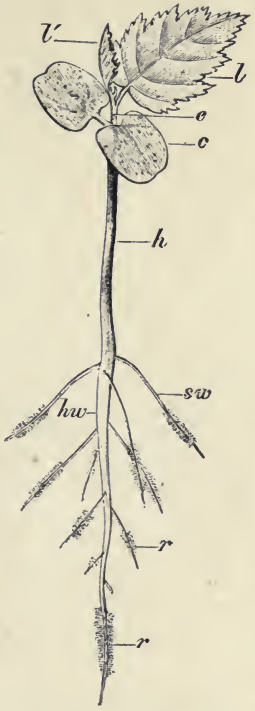


FIG. 194. Seedling of hazel (*Carpinus*), showing primary root (*hw*) bearing rootlets (*sw*) upon which are numerous root hairs (*r*), hypocotyl (*h*), cotyledons (*c*), young stem (*e*), and first (*l*) and second (*l'*) true leaves.—After SCHIMPER.

(3) The female gametophyte produces no archegonia, but a single naked egg.

CHAPTER XIII

THE FLOWER

119. **General characters.**—In general the flower may be regarded as a modified branch of the sporophyte stem bearing sporophylls and usually floral leaves. Its representative among the Pteridophytes and Gymnosperms is the strobilus, which has sporophylls but not floral leaves. Among Angiosperms it begins in a simple and somewhat indefinite way, gradually becomes more complex and modified, until it appears as an elaborate structure very efficient for its purpose.

This evolution of the flower has proceeded along many lines, and has resulted in endless diversity of structure. These diversities are largely used in the classification of Angiosperms, as it is supposed that near relatives are indicated by similar floral structures, as well as by other features. The significance of these diversities is supposed to be connected with securing proper pollination, chiefly by insects, and favorable seed distribution.

Although the evolution of flowers has proceeded along several lines simultaneously, now one feature and now another being emphasized, it will be clearer to trace some of the important lines separately.

120. **Floral leaves.**—In the simplest flowers floral leaves do not appear, and the flower is represented only by the sporophylls. Both kinds of sporophylls may be associated, in which case the flower is said to be *perfect* (Fig. 195); or they may not both occur in the same flower, in which case one flower is *staminate* and the other *pistillate* (Fig. 196).

When the floral leaves first appear in connection with the sporophylls they are inconspicuous, scale-like bodies. In higher forms they become more prominent and inclose

FIG. 195. Lizard's tail (*Saururus*): *A*, tip of branch bearing leaves and elongated cluster of flowers; *B*, a single naked flower from *A*, showing stamens and four spreading and stigmatic styles; *C*, flower from another species, showing subtending bract, absence of floral leaves, seven stamens, and a syncarpous pistil; the flowers naked and perfect.—After ENGLER.

FIG. 196. Naked flowers of different willows (*Salix*), each from the axil of a bract: *a*, *b*, *c*, staminate flowers; *d*, *e*, *f*, pistillate flowers, the pistil composed of two carpels (syncarpous). — After WARMING.

FIG. 197. Flower of calamus (*Acorus*), showing simple perianth, stamens, and syncarpous pistil: a hypogynous flower without differentiation of calyx and corolla.—After ENGLER.

FIG. 198. Flowers of elm (*Ulmus*): *A*, branch bearing clusters of flowers and scaly buds; *B*, single flower, showing simple perianth and stamens, being a staminate flower; *C*, flower showing perianth, stamens, and the two divergent styles stigmatic on inner surface, being a perfect flower; *D*, section through perfect flower, showing perianth, stamens, and pistil with two loculi each with a single ovule —After ENGLER.

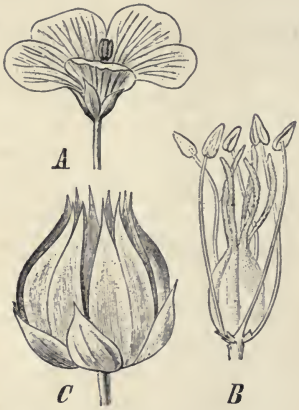


FIG. 199. Common flax (*Linum*): *A*, entire flower, showing calyx and corolla; *B*, floral leaves removed, showing stamens and syncarpous pistil; *C*, a mature capsule splitting open. — After SCHIMPER.

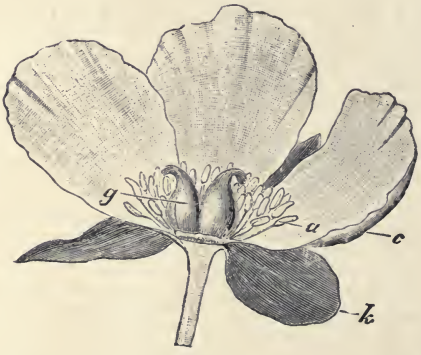


FIG. 200. A flower of peony, showing the four sets of floral organs: *k*, the sepals, together called the calyx; *c*, the petals, together called the corolla; *a*, the numerous stamens; *g*, the two carpels, which contain the ovules.—After STRASBURGER.

the young sporophylls, but they are all alike, forming what is called the *perianth* (Figs. 197, 198).

In still higher forms the perianth differentiates, the inner floral leaves become more delicate in texture, larger and generally brightly colored (Fig. 199, *A*). The outer set may remain scale-like, or become like small foliage leaves. When the differentiation of the perianth is distinct, the outer set of floral leaves is called the *calyx*, each leaf being a *sepal;* the inner set is the *corolla*, each leaf being a *petal* (Fig. 200). Sometimes, as in the lily, all the floral leaves become uniformly large and brightly colored, in which case the term perianth is retained (Fig. 201). In other cases, the calyx may be the large and colored set, but whenever there is a clear distinction between sets, the outer is the calyx, the inner the corolla.

FIG. 201. — An easter-lily, a Monocotyledon, showing perianth (*a*), stamens (*b*), stigma (*c*), flower bud (*d*), and a carpel after the perianth has fallen (*l*), with its knob-like stigma, long style, and slender ovary.—CALDWELL.

Both floral sets may not appear, and it has become the custom to regard the missing set as the corolla, such flowers being called *apetalous*, meaning

"without petals." It is not always possible to tell whether a flower is apetalous—that is, whether it has lost a floral set which it once had—or is simply one whose perianth has not yet differentiated, in which case it would be a "primitive type."

The line of evolution, therefore, extends from flowers without floral leaves, or *naked flowers*, to those with a distinctly differentiated calyx and corolla.

121. **Spiral to cyclic flowers.**—In the simplest flowers the sporophylls and floral leaves (if any) are distributed about an elongated axis in a spiral, like a succession of leaves. That part of the axis which bears the floral organs is for convenience called the *receptacle* (Fig. 202). As the recep-

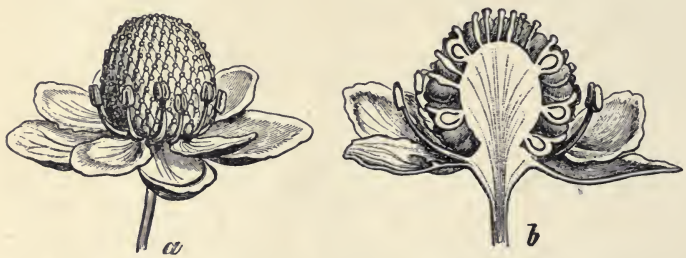


FIG. 202. A buttercup (*Ranunculus*): *a*, complete flower, showing sepals, petals, stamens, and head of numerous carpels on a large receptacle; *b*, section showing relation of parts; a hypogynous, polypetalous, apocarpous, actinomorphic flower. —After BAILLON.

tacle is elongated and capable of continued growth, an indefinite number of each floral organ may appear, especially of the sporophylls. With the spiral arrangement, therefore, there is no definiteness in the number of floral organs; there may be one or very many floral leaves, or stamens, or carpels. The spiral arrangement and indefinite numbers are features of the ordinary strobilus, and therefore such flowers are regarded as more primitive than the others.

In higher forms the receptacle becomes shorter, the spiral more closely coiled, until finally the sets of organs

appear to be thrown into rosettes or cycles. This change does not necessarily affect all the parts simultaneously. For example, in the common buttercup the sepals and petals are nearly in cycles, while the carpels are spirally arranged and indefinitely numerous on the head-like receptacle (Fig. 202). On the other hand, in the common water-

Fig. 203. Flower of water-lily (*Nymphæa*), showing numerous petals and stamens.—After Caspary.

lily the petals and stamens are spiral, and indefinitely repeated, while the sepals and carpels are approximately cyclic (Fig. 203).

Finally, in the highest forms, all the floral organs are in definite cycles, and there is no indefinite repetition of any part. All through this evolution from the spiral to the cyclic arrangement there is constantly appearing a tendency to "settle down" to certain definite numbers. When the complete cyclic arrangement is finally established these numbers are established, and they are characteristic of great groups. In cyclic Monocotyledons there are nearly always just three organs in each cycle, forming what is called a *trimerous* flower (Fig. 204); while in cyclic Dicot-

yledons the number five prevails, but often four appears, forming *pentamerous* or *tetramerous* flowers (Fig. 199). This does not mean that there are necessarily just three, four, or five of each organ in the flower, for there may be two or more cycles of some one organ. For example, in the common lily there are six floral leaves in two sets, six stamens in two sets, and three carpels (Fig. 204).

In the cyclic flowers it is also to be noted that each set alternates with the next set outside (Fig. 204). The petals are not directly opposite the sepals, but are opposite the spaces between sepals; the stamens in turn alternate with the petals; if there is a second set of stamens, it alternates with the outer set, and so on. If two adjacent sets are found opposing one another, it is usually due to the fact that a set between has disappeared. For example, if a set of stamens is opposite the set of petals, either an outer stamen set or an inner petal set has disappeared.

Fig. 204. Diagram of such a flower as the lily, showing relation of parts: uppermost organ is the bract in the axil of which the flower occurs; black dot below indicates position of stem; floral parts in threes and in five alternating cycles (two stamen sets), being a trimerous, pentacyclic flower.—After Schimper.

This line of evolution, therefore, extends from flowers whose parts are spirally arranged upon an elongated receptacle and indefinite in number, to those whose parts are in cycles and definite in number.

122. **Hypogynous to epigynous flowers.**—In the simpler flowers the sepals, petals, and stamens arise from beneath the ovary (Figs. 197, 202, 205, *1*). As in such cases the ovary or ovaries may be seen distinctly above the origin (*insertion*) of the other parts, such a flower is often said to have a "superior ovary." The more usual term, however, is *hypogynous*, meaning in effect "under the ovary," refer-

ring to the fact that the insertion of the other parts is under the ovary.

Hypogyny is very largely displayed among flowers, but there is to be observed a tendency in some to carry the insertion of the outer parts higher up. When the outer parts arise from the rim of an urn-like outgrowth from the

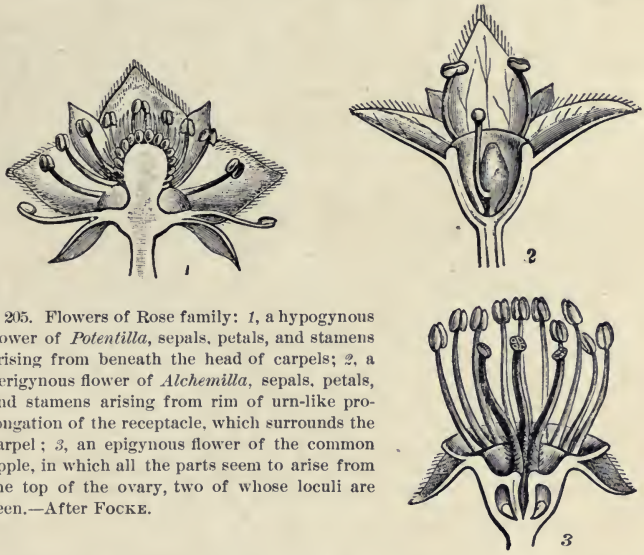


FIG. 205. Flowers of Rose family: *1*, a hypogynous flower of *Potentilla*, sepals, petals, and stamens arising from beneath the head of carpels; *2*, a perigynous flower of *Alchemilla*, sepals, petals, and stamens arising from rim of urn-like prolongation of the receptacle, which surrounds the carpel; *3*, an epigynous flower of the common apple, in which all the parts seem to arise from the top of the ovary, two of whose loculi are seen.—After FOCKE.

receptacle, which surrounds the pistil or pistils, the flower is said to be *perigynous* (Figs. 205, *2*, 206), meaning "around the pistil." Finally, the insertion is carried above the ovary, and sepals, petals, and stamens seem to arise from the top of the ovary (Fig. 205, *3*), such a flower being *epigynous*, the outer parts appearing "upon the ovary." In such a case the ovary does not appear within the flower, but below it (Figs. 205, 252, 261), and the flower is often said to have an "inferior ovary."

123. **Apocarpous to syncarpous flowers.**—In the simpler flowers the carpels are entirely distinct, each carpel organ-

izing a simple pistil, a single flower containing as many pistils as there are carpels, as in the buttercups (Figs. 200, 202). Such a flower is said to be *apocarpous*, meaning "carpels separate." There is a very strong tendency,

FIG. 206. Sweet-scented shrub (*Calycanthus*): *A*, tip of branch bearing flowers; *B*, section through flower, showing numerous floral leaves, stamens, and carpels, and also the development of the receptacle about the carpels, making a perigynous flower.—After THIEBAULT.

however, for the carpels of a flower to organize together and form a single compound pistil. In such a flower there may be several carpels, but they all appear as one organ (Figs. 195, *C*, 197, 198, *D*, 199, *B*), and the flower is said to be *syncarpous*, meaning "carpels together."

124. **Polypetalous to sympetalous flowers.**—The tendency for parts of the same set to coalesce is not confined to the carpels. Sepals often coalesce (Fig. 208), and sometimes stamens, but the coalescence of petals seems to be more important. Among the lower forms the petals are entirely separated (Figs. 199, *A*, 202, 203, 207), a condition which

has received a variety of names, but probably the most common is *polypetalous*, meaning "petals many," although *eleutheropetalous*, meaning "petals free," is much more to the point.

FIG. 207. Flower of strawberry, showing sepals, petals, numerous stamens, and head of carpels; the flower is actinomorphic, hypogynous, and with no coalescence of parts.—After BAILEY.

In the highest Angiosperms, however, the petals are coalesced, forming a more or less tubular organ (Figs. 208–210). Such flowers are said to be *sympetalous*, meaning "petals united." The words *gamopetalous* and *monopetalous* are also much used, but all three words refer to the same condition of the flower. Often the sympetalous corolla is differenti-

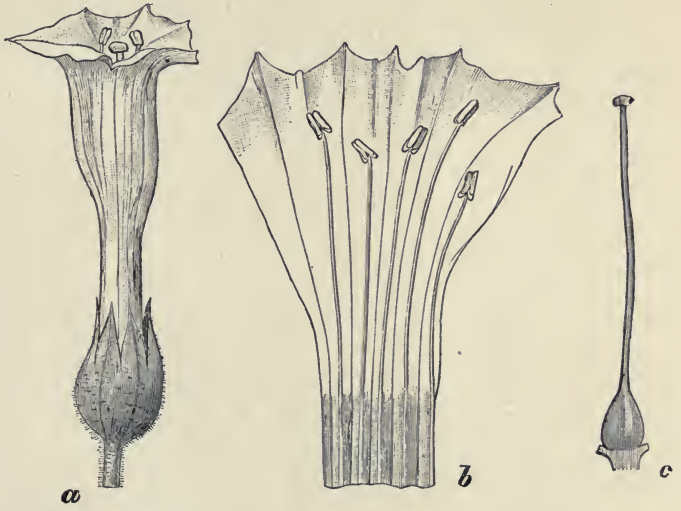


FIG. 208. A flower of the tobacco plant: *a*, a complete flower, showing the calyx with its sepals blended below, the funnelform corolla made up of united petals, and the stamens just showing at the mouth of the corolla tube; *b*, a corolla tube split open and showing the five stamens attached to it near the base; *c*, a syncarpous pistil made up of two carpels, showing ovary, style, and stigma.—After STRASBURGER.

ated into two regions (Fig. 210, *b*), a more or less tubular portion, the *tube*, and a more or less flaring portion, the *limb*.

Fig. 209. Flower of morning-glory (*Ipomœa*), with sympetalous corolla split open, showing the five attached stamens, and the superior ovary with prominent style and stigma; the flower is hypogynous, sympetalous, and actinomorphic.—After Meissner.

125. **Actinomorphic to zygomorphic flowers.**—In the simpler flowers all the members of any one cycle are alike; the petals are all alike, the stamens are all alike, etc. Looking at the center of the flower, all the parts are repeated about it like the parts of a radiate animal. Such a flower is *actinomorphic*, meaning "radiate," and is often called a "regular flower." Although the term actinomorphic strictly applies to all the floral organs, it is especially noteworthy in connection with the corolla, whose changes will be noted.

Fig. 210. A group of sympetalous flower forms: *a*, a flower of harebell, showing a bell-shaped corolla; *b*, a flower of phlox, showing a tube and spreading limb; *c*, a flower of dead-nettle, showing a zygomorphic two-lipped corolla; *d*, a flower of toad-flax, showing a two-lipped corolla, and also a spur formed by the base of the corolla; *e*, a flower of the snapdragon, showing the two lips of the corolla closed. —After Gray.

In many cases the petals are not all alike, and the radiate character, with its similar parts repeated about a center, is lost. In the common violet, for example, one of the petals develops a spur (Fig. 211); in the sweet pea the petals are remarkably unlike, one being broad and erect, two smaller and drooping downward, and the other two much modified to form together a boat-like structure which incloses the sporophylls. Such flowers are called *zygomorphic*, meaning "yoke-form," and they are often called "irregular flowers."

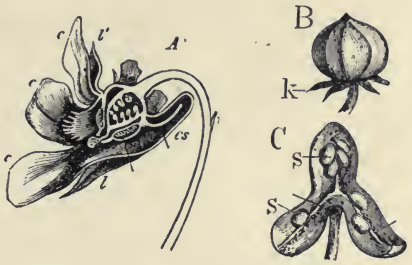


Fig. 211. The pansy (*Viola tricolor*): *A*, section showing sepals (*l*, *l'*), petals (*c*) one of which produces a spur (*cs*), the flower being zygomorphic; *B*, mature fruit (a capsule) and persistent calyx (*k*); *C*, the three boat-shaped valves of the fruit open, most of the seeds (*s*) having been discharged.—After Sachs.

When zygomorphic flowers are also sympetalous the corolla is often curiously shaped. A very common form

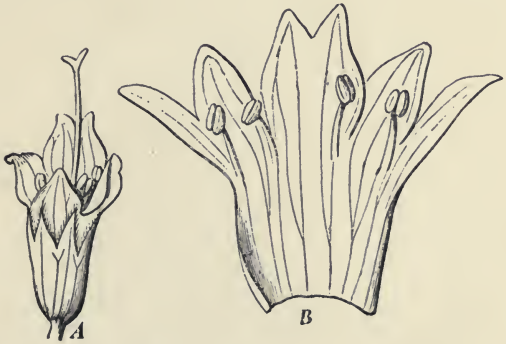


Fig. 212. Flower of a mint (*Mentha aquatica*): *A*, the entire flower, showing calyx of united sepals, unequal petals, stamens, and style with two stigma lobes; *B*, a corolla split open, showing petals united and the four stamens attached to the tube; the flower is sympetalous and zygomorphic.—After Wermng.

is the *bilabiate*, or "two-lipped," in which two of the petals usually organize to form one lip, and the other three form the other lip (Figs. 210, *c*, *d*, *e*, 212, 213). The two lips may be nearly equal, the upper may stand high or overarch the lower, the lower may project more or less conspicuously, etc.

FIG. 213. Flower of a Labiate (*Teucrium*), showing the calyx of coalesced sepals, the sympetalous and two-lipped (bilabiate) corolla with three petals (middle one largest) in the lower lip and two small ones in the upper, and the stamens and style emerging through a slit on the upper side of the tube; a sympetalous and zygomorphic flower.—After BRIQUET.

126. **Inflorescence.**—Very often flowers are solitary, either on the end of a stem or branch (Figs. 231, 236), or in the axil of a leaf (Fig. 258). But such cases grade insensibly into others where a definite region of the plant is set aside to produce flowers (Figs. 253, 260). Such a region forms what is called the *inflorescence*. The various ways in which flowers are arranged in an inflorescence have received technical names, but they do not enter into our purpose here. They are simply different ways in which plants seek to display their flowers so as to favor pollination and seed distribution.

There are several tendencies, however, which may be noted. Some groups incline to loose clusters, either elongated (Fig. 260) or flat-topped (Fig. 253); others prefer large and often solitary flowers (Fig. 258) to a cluster of smaller ones; but in the highest groups there is a distinct tendency to reduce the size of the flowers, increase their number, and mass them into a compact cluster. This tendency reaches its highest expression in the greatest family of the Angiosperms, the Compositæ, of which the sunflower or dandelion can be taken as an illustration (Figs. 261, 262), in which numerous small flowers are closely packed together in a compact cluster which resembles a single large flower. It does not follow that all very compact inflorescences in-

dicate plants of high rank, for the cat-tail flag (Fig. 221) and many grasses have very compact inflorescences, and they are supposed to be plants of low rank. It is to be noted, however, that the very highest groups have settled upon this as the best type of inflorescence.

127. **Summary.**—In tracing the evolution of flowers, therefore, the following tendencies become evident: (1) from naked flowers to those with distinct calyx and corolla; (2) from spiral arrangement and indefinite numbers to cyclic arrangement and definite numbers; (3) from hypogynous to epigynous flowers; (4) from apocarpous to syncarpous pistils; (5) from polypetalous to sympetalous corollas; (6) from actinomorphic or regular to zygomorphic or irregular flowers; (7) from loose to compact inflorescences.

These various lines appear in all stages of advancement in different flowers, so that it would be impossible to determine the relative rank in all cases. However, if a flower is naked, spiral, with indefinite numbers, hypogynous, and apocarpous, it would certainly rank very low. On the contrary, the flowers of the Compositæ have calyx and corolla, are cyclic, epigynous, syncarpous, sympetalous, often zygomorphic, and are in a remarkably compact inflorescence, indicating the highest possible combination of characters.

128. **Flowers and insects.** — The adaptations between flowers and insects, by which the former secure pollination and the latter food, are endless. Many Angiosperm flowers, especially those of the lower groups, are still anemophilous, as are the Gymnosperms, but most of them, by the presence of color, odor, and nectar, indicate an adaptation to the visits of insects. This wonderful chapter in the history of plants will be found discussed, with illustrations, in *Plant Relations*, Chapter VII.

CHAPTER XIV

MONOCOTYLEDONS AND DICOTYLEDONS

129. **Contrasting characters.**—The two great groups of Angiosperms are quite distinct, and there is usually no difficulty in recognizing them. The monocotyledons are usually regarded as the older and the simpler forms, and are represented by about twenty thousand species. The Dicotyledons are much more abundant and diversified, containing about eighty thousand species, and form the dominant vegetation almost everywhere. The chief contrasting characters may be stated as follows:

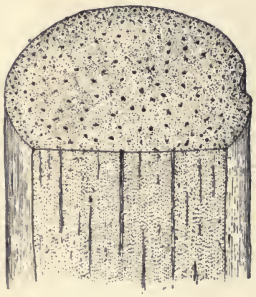


FIG. 214. Section of stem of corn, showing the scattered bundles, indicated by black dots in cross-section, and by lines in longitudinal section. —From "Plant Relations."

Monocotyledons. — (1) Embryo with terminal cotyledon and lateral stem-tip. This character is practically without exception.

(2) Vascular bundles of stem scattered (Fig. 214). This means that there is no annual increase in the diameter of the woody stems, and no extensive branching, but to this there are some exceptions.

(3) Leaf veins forming a closed system (Fig. 215, figure to left). As a rule there is an evident set of veins which run approximately parallel, and intricately branching between them is a system of minute veinlets not readily seen. The vein system does not end freely in the

margin of the leaf, but forms a "closed venation," so that the leaves usually have an even (*entire*) margin. There are some notable exceptions to this character.

(4) Cyclic flowers trimerous. The "three-parted"

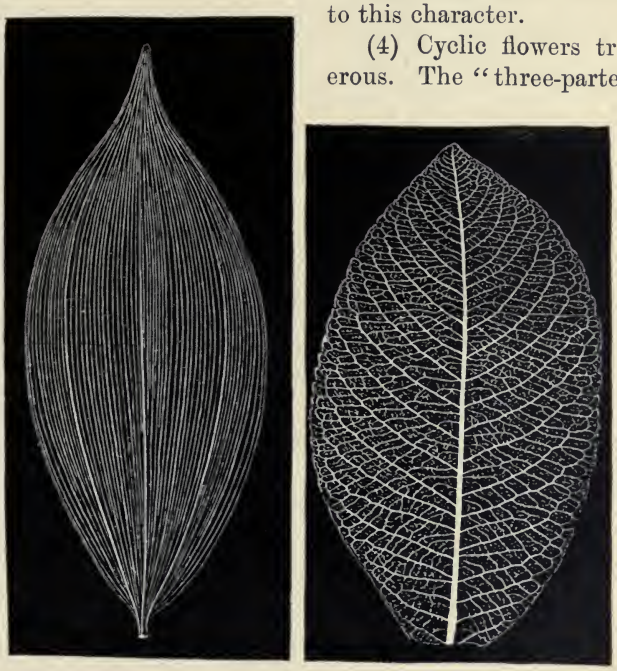


Fig. 215. Two types of leaf venation: the figure to the left is from Solomon's seal, a Monocotyledon, and shows the principal veins parallel, the very minute cross veinlets being invisible to the naked eye; that to the right is from a willow, a Dicotyledon, and shows netted veins, the main central vein (midrib) sending out a series of parallel branches, which are connected with one another by a network of veinlets.—After Ettingshausen.

flowers of cyclic Monocotyledons are quite characteristic, but there are some trimerous Dicotyledons.

Dicotyledons.—(1) Embryo with lateral cotyledons and terminal stem-tip.

(2) Vascular bundles of stem forming a hollow cylinder (Fig. 216, *w*). This means an annual increase in the diam-

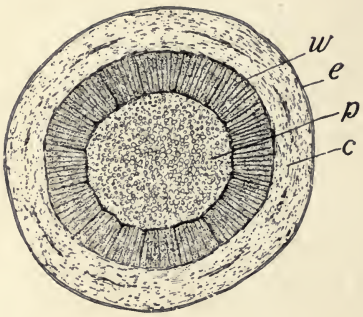


Fig. 216. Section across a young twig of box elder, showing the four stem regions: *e*, epidermis, represented by the heavy bounding line; *c*, cortex; *w*, vascular cylinder; *p*, pith.—From "Plant Relations."

eter of woody stems (Fig. 217, *w*), and a possible increase of the branch system and foliage display each year.

(3) Leaf veins forming an open system (Fig. 215, figure to right). The network of smaller veinlets between the larger veins is usually very evident, especially on the under surface of the leaf, suggesting the name "net-veined" leaves, in contrast to the "parallel-veined" leaves of Monocotyledons. The vein system ends freely in the margin of the leaf, forming an "open venation." In consequence of this, although the leaf may remain entire, it very commonly becomes toothed, lobed, and divided in various ways. Two main types of venation may be noted, which influence the form of leaves. In one case a single very prominent vein (*rib*) runs through the middle of the blade, and is called the *midrib*. From this all the minor veins arise as branches (Figs. 218, 219), and such a leaf

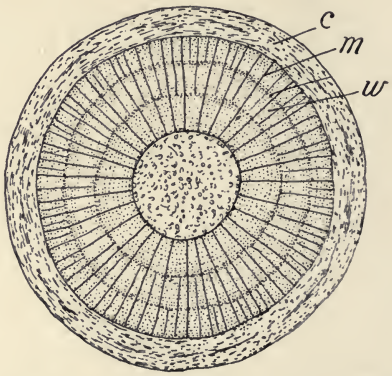


Fig. 217. Section across a twig of box elder three years old, showing three annual rings, or growth rings, in the vascular cylinder; the radiating lines (*m*) which cross the vascular region (*w*) represent the pith rays, the principal ones extending from the pith to the cortex (*c*).—From "Plant Relations."

is said to be *pinnate* or *pinnately veined*, and inclines to elongated forms. In the other case several ribs of equal prominence enter the blade and diverge through it (Fig. 218). Such a leaf is *palmate* or *palmately veined*, and inclines to broad forms.

(4) Cyclic flowers pentamerous or tetramerous. The flowers "in fives" are greatly in the majority, but some

FIG. 218. Leaves showing pinnate and palmate branching; the one to the left is from sumach, that to the right from buckeye.—CALDWELL.

very prominent families have flowers "in fours." There are also dicotyledonous families with flowers "in threes," and some with flowers "in twos."

It should be remembered that no one of the above characters, unless it be the character of the embryo, should be depended upon absolutely to distinguish these two groups.

It is the combination of characters which determines a group.

Monocotyledons

130. **Introductory.**—This great group gives evidence of several distinct lines of development, distinguished by what may be called the working out of different ideas. In this way numerous *families* have resulted—that is, groups of

Fig. 219. A leaf of honey locust, to show twice pinnate branching (bipinnate leaf).—Caldwell.

forms which seem to belong together on account of similar structures. This similarity of structure is taken to mean relationship. A family, therefore, is made up of a group of nearly related forms. Opinions may differ as to what forms are so nearly related that they deserve to constitute a distinct family. A single family of some botanists may be "split up" into two or more families by others. Despite this diversity of opinion, most of the families are fairly well recognized.

Within a family there are smaller groups, indicating closer relationships, known as *genera* (singular, *genus*). For example, in the great family to which the asters belong, the different asters resemble one another more than they do any other members of the family, and hence are grouped together in a genus *Aster*. In the same family the goldenrods are grouped together in the genus *Solidago*. The different kinds of *Aster* or of *Solidago* are called *species* (singular also *species*). A group of related *species*, therefore, forms a *genus;* and a group of related *genera* forms a *family*.

The technical name of a plant is the combination of its generic and specific names, the former always being written first. For example, *Quercus alba* is the name of the common white oak, *Quercus* being the name of the genus to which all oaks belong, and *alba* the specific name which distinguishes this oak from other oaks. No other names are necessary, as no two genera of plants can bear the same name.

In the Monocotyledons about forty families are recognized, containing numerous genera, and among these genera the twenty thousand species are distributed. It is evident that it will be impossible to consider such a vast array of forms, even the families being too numerous to mention. A few important families will be mentioned, which will serve to illustrate the group.

131. **Pondweeds.**—These are submerged aquatics, found in most fresh waters (some are marine), and are regarded as among the simplest Monocotyledons. They are slender, branching herbs, growing under water, but often having floating leaves, and sending the simple flowers or flower clusters above the surface for pollination and seed-distribution. The common pondweed (*Potamogeton*) contains numerous species (Fig. 220), while *Naias* (naiads) and *Zannichellia* (horned pondweed) are common genera in ponds and slow waters.

The simple character of these forms is indicated by their aquatic habit and also by their flowers, which are mostly naked and with few sporophylls. A flower may consist of a single stamen, or a single carpel; or there may be several stamens and carpels associated, but without any coalescence (Fig. 220, *B*).

In the same general line with the pondweeds, but with more complex flowers, are the genera *Sagittaria* (arrow-

FIG. 220. Pondweed (*Potamogeton*): *A*, branch with cluster (spike) of simple flowers, showing also the broad floating leaves and the narrow submerged ones; *B*, a single flower, showing the inconspicuous perianth lobes (*c*), the short stamens (*a*), and the two short styles with conspicuous stigmatic surfaces.—*A* after REICHENBACH; *B* after LE MAOUT and DECAISNE.

FIG. 221. Cat-tails (*Typha*), showing the dense spikes of very simple flowers, each showing two regions, the lower the pistillate flowers, the upper the staminate.—From "Field, Forest, and Wayside Flowers."

leaf) and *Alisma* (water-plantain), in which there is a distinct calyx and corolla. The genus *Typha* (cat-tail) is also an aquatic or marsh form of very simple type, the flowers being in dense cylindrical clusters (*spikes*), the upper flowers consisting of stamens, the lower of carpels, thus forming two very distinct regions of the spike (Fig. 221).

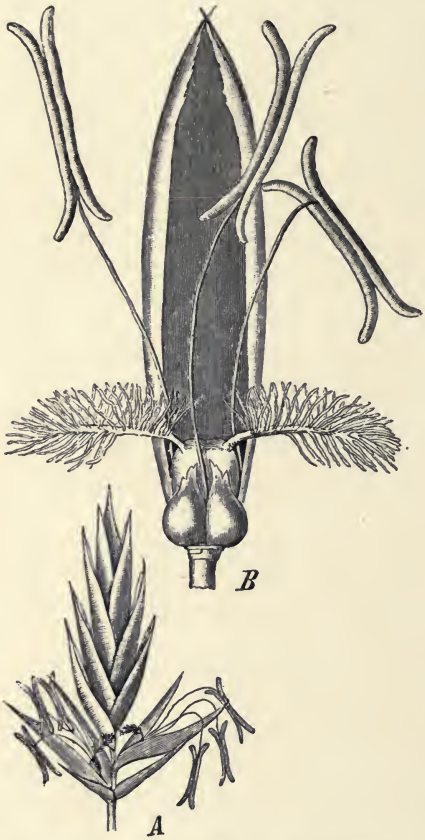


FIG. 222. A common meadow grass (*Festuca*): *A*, portion of flower cluster (spikelet), showing the bracts, in the axils of two of which flowers are exposed; *B*, a single flower with its enveloping bract, showing three stamens, and a pistil whose ovary bears two style branches with much branched stigmas.—After STRASBURGER.

132. **Grasses.**— This is one of the largest and probably one of the most useful groups of plants, as well as one of the most peculiar. It is world-wide in its distribution, and is remarkable in its display of individuals, often growing so densely over large areas as to form a close turf. If the grass-like sedges be associated with them there are about six thousand species, representing nearly one third of the Monocotyledons. Here belong the various cereals, sugar canes,

bamboos, and pasture grasses, all of them immensely useful plants.

The flowers are very simple, having no evident perianth (Fig. 222). Most commonly a flower consists of three stamens, surrounding a single carpel, whose ovary ripens into the *grain*, the characteristic seed-like fruit of the group. The stamens, however, may be of any number from one to six. The flowers, therefore, are naked, with indefinite numbers, and hypogynous, indicating a comparatively simple type. It is also noteworthy that the group is anemophilous.

One of the noteworthy features of the group is the prominent development of peculiar leaves (*bracts*) in connection with the flowers. Each flower is completely protected or even inclosed by one of these bracts, and as the bracts usually overlap one another the flowers are invisible until the bracts spread apart and permit the long dangling stamens to show themselves. These bracts form the so-called "chaff" of wheat and other cereals, where they persist and more or less envelop the grain (ripened ovary). As they are usually called *glumes*, the grasses and sedges are said to be *glumaceous* plants.

Grasses are not always lowly plants, for in the tropics the bamboos and canes form growths that may well be called forests. The grasses constitute the family *Gramineæ*, and the sedges the family *Cyperaceæ*.

133. **Palms.**—More than one thousand species of palms are grouped in the family *Palmaceæ*. These are the tree Monocotyledons, and are very characteristic of the tropics, only the palmetto getting as far north as our Gulf States. The habit of body is like that of tree-ferns and Cycads, a tall unbranched columnar trunk bearing at its summit a crown of huge leaves which are pinnate or palmate in character, and often splitting so as to appear lobed or compound (Figs. 223, 224).

The flower clusters are usually very large (Fig. 223), and each cluster at first is inclosed in a huge bract, which

Fig. 223. A date palm, showing the unbranched columnar trunk covered with old leaf bases, and with a cluster of huge pinnate leaves at the top, only the lowest portions of which are shown; two of the very heavy fruit clusters are also shown.—From "Plant Relations,"

is often hard. Usually a perianth is present, but with no differentiation of calyx and corolla, and the flower parts are quite definitely in "threes," so that the cyclic arrangement with the characteristic Monocotyledon number appears.

Fig. 224. A fan palm, with low stem and crown of large palmate leaves, which have split so as to appear palmately branched.—From "Plant Relations."

134. **Aroids.**—This is a group of nearly one thousand species, most of them belonging to the family *Araceæ*. In our flora the Indian turnip or Jack-in-the-pulpit (*Arisæma*) (Fig. 225), sweetflag (*Acorus*), and skunk-cabbage (*Symplocarpus*), may be taken as representatives; while the cultivated Calla-lily is perhaps even better known. The great display of aroids, however, is in the tropics, where they are endlessly modified in form and structure, and are erect, or climbing, or epiphytic.

The flowers are usually very simple, often being naked, with two to nine stamens, and one to four carpels (Fig.

FIG. 225. Jack-in-the-pulpit (*Arisæma*), showing the overarching spathes; in one case a side view shows the naked tip of the projecting spadix.—After ATKINSON.

197). They are inconspicuous and closely set upon the lower part of a fleshy axis, which is naked above and often

modified in a remarkable way into a club-shaped or tail-like often brightly colored affair. This singular flower-cluster with its fleshy axis is called a *spadix*. The flowers often include but one sort of sporophyll, and staminate and pistillate flowers hold different positions upon the spadix (Fig. 226).

The spadix is enveloped by a great bract, which surrounds and overarches like a large loose hood, and is called the *spathe*. The spathe is exceedingly variable in form, and is often conspicuously colored, forming in the Calla-lily the conspicuous white part, within which the spadix may be seen, near the base of which the flowers are found. In Jack-in-the-pulpit (Fig. 225) it is the overarching spathe which suggests the "pulpit." The spadix and spathe are the characteristic features of the group, and the spathe is variously modified in form, structure, and color for insect pollination, as is the perianth of other entomophilous groups.

FIG. 226. Spadix of an *Arum*, with spathe removed, showing cluster of naked pistillate flowers at base, just above a cluster of staminate flowers, and the club-shaped tip of the spadix.—After WOSSIDLO.

Aroids are further peculiar in having broad net-veined leaves of the Dicotyledon type. Altogether they form a remarkably distinct group of Monocotyledons.

135. **Lilies.**—The lily and its allies are usually regarded as the typical Monocotyledon forms. The perianth is fully developed, and is very conspicuous, either undifferentiated or with distinct calyx and corolla, and the flower is well organized for insect pollination. The flowers are either solitary or few in a cluster and correspondingly large, or in more compact clusters and smaller. In any event, the perianth is the conspicuous thing, rather than spathes or glumes.

In the general lily alliance, composed of eight or nine families, there are more than four thousand species, representing about one fifth of all the Monocotyledons, and they are distributed everywhere. They are almost all terrestrial herbs, and are prominently *geophilous* ("earth-lovers")—that is, they develop bulbs, rootstocks, etc., which enable them to disappear from above the surface during unfavorable conditions (cold or drought), and then to reappear rapidly upon the return of favorable conditions (Figs. 227, 228, 231, 233).

Fig. 227. Wake-robin (*Trillium*), showing rootstock, from which two branches arise, each bearing a cycle (whorl) of three leaves and a single trimerous flower.—After Atkinson.

In the regular lily family (*Liliaceæ*) the flowers are hypogynous and actinomorphic (Fig. 231), the six perianth parts are mostly alike and sometimes sympetalous (as in the lily-of-the-valley, hyacinth, easter lily) (Figs. 201, 229), the stamens are usually six (two sets), and the three carpels are syncarpous (Figs. 204, 230). This is a higher combination of floral characters than any of the preceding groups presents. Hypogyny and actinomorphy are low, but a conspicuous perianth, syncarpy, and occasional sympetaly indicate considerable advancement.

In the amaryllis family (*Amaryllidaceæ*), a higher family of the same general line, represented by species of *Narcissus* (jonquils, daffodils, etc.), *Agave*, etc., the flowers are distinctly epigynous.

FIG. 228. Star-of-Bethlehem (*Ornithogalum*): *a*, entire plant with tuberous base and trimerous flowers; *b*, a single flower; *c*, portion of flower showing relation of parts, perianth lobes and stamens arising from beneath the prominent ovary (hypogynous); *d*, mature fruit; *e*, section of the syncarpous ovary, showing the three carpels and loculi.—After SCHIMPER.

In the iris family (*Iridaceæ*), the most highly specialized family of the lily line, and represented by the various spe-

Fig. 229. The Japan lily, showing a tubular perianth, the parts of the perianth distinct above.—From "Field, Forest, and Wayside Flowers."

cies of *Iris* (flags) (Fig. 232), *Crocus*, *Gladiolus* (Figs. 233, 234), etc., the flowers are not only epigynous, but some of them are zygomorphic. When a plant has reached both epigyny and zygomorphy in its flowers, it may be regarded as of high rank.

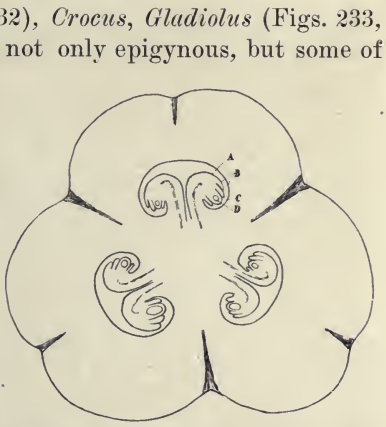


FIG. 230. Diagrammatic cross-section of ovary of *Lilium Philadelphicum*, showing the three loculi, in each of which are two ovules (megasporangia); *A*, ovule; *B*, integuments; *C*, nucellus; *D*, embryo-sac (megaspore).—CALDWELL.

136. **Orchids.**—In number of species this (*Orchidaceæ*) is the greatest family among the Monocotyledons, the species being variously estimated from six thousand to ten thousand, representing between one third and one half of all known Monocotyledons. In display of individuals, however, the orchids are not to be compared with the grasses, or even with lilies, for the various species are what are called "rare plants"—that is, not extensively distributed, and often very much restricted. Although there are some beautiful orchids in temperate regions, as species of *Habenaria* (rein-orchis) (Fig. 235), *Pogonia*, *Calopogon*, *Calypso*, *Cypripedium* (lady-slipper, or moccasin flower) (Fig. 236), etc., by far the greatest display and diversity are in the tropics, where many of them are brilliantly flowered epiphytes (Fig. 237).

Orchids are the most highly specialized of Monocotyledons, and their brilliant coloration and bizarre forms are associated with marvelous adaptation for insect visitation (see *Plant Relations*, pp. 134, 135). The flowers are epigynous and strongly zygomorphic. One of the petals is remarkably modified, forming a conspicuous *lip* which is

FIG. 231. The common dog-tooth violet, showing the large mottled leaves and conspicuous flowers which are sent rapidly above the surface from the subterranean bulb (see cut in the left lower corner), also some petals and stamens and the pistil dissected out.—From "Plant Relations."

Fig. 232. Flower of flag (*Iris*), showing some of the sepals and petals, one of the three stamens, and the distinctly inferior ovary, being an epigynous flower.—After Gray.

modified in a great variety of ways, and a prominent, often very long, *spur*, in the bottom of which nectar is secreted, which must be reached by the proboscis of an insect (Fig. 235). The stamens are reduced to one or two, and welded with the style

Fig. 234. Flower cluster of *Gladiolus*, showing somewhat zygomorphic flowers.—Caldwell.

Fig. 233. *Gladiolus*, showing tuberous subterranean stem from which roots descend, grass-like leaves, and somewhat zygomorphic flowers.—After Reichenbach.

and stigmatic surface into an indistinguishable mass in the center of the flowers. The pollen-grains in each sac are sticky and cohere in a club-shaped mass (*pollinium*), which is pulled out and carried to another flower by the

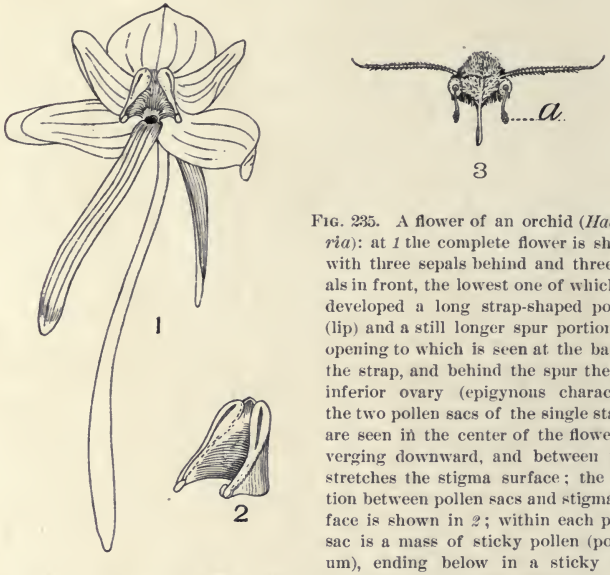


FIG. 235. A flower of an orchid (*Habenaria*): at *1* the complete flower is shown, with three sepals behind and three petals in front, the lowest one of which has developed a long strap-shaped portion (lip) and a still longer spur portion, the opening to which is seen at the base of the strap, and behind the spur the long inferior ovary (epigynous character); the two pollen sacs of the single stamen are seen in the center of the flower, diverging downward, and between them stretches the stigma surface; the relation between pollen sacs and stigma surface is shown in *2*; within each pollen sac is a mass of sticky pollen (pollinium), ending below in a sticky disk, which may be seen in *1* and *2*; in *3* a pollen mass (*a*) is shown sticking to each eye of a moth.—After GRAY.

visiting insect. The whole structure indicates a very highly specialized type, elaborately organized for insect pollination.

Another interesting epigynous and zygomorphic tropical group, but not so elaborate as the orchids, is represented by the cannas and bananas (Fig. 120), common in cultivation as foliage plants, and the aromatic gingers.

From the simple pondweeds to the complex orchids the evolution of the Monocotyledons has proceeded, and between them many prominent and successful families have been worked out.

Fig. 236. A clump of lady-slippers (*Cypripedium*), showing the habit of the plant and the general structure of the zygomorphic flower.—After Gibson.

FIG. 237. A group of orchids (*Cattleya*), showing the very zygomorphic flowers, the lip being well shown in the flower to the left (lowest petal).—CALDWELL.

DICOTYLEDONS

137. **Introductory.**—Dicotyledons form the greatest group of plants in rank and in numbers, being the most highly organized, and containing about eighty thousand species. They represent the dominant and successful vegetation in all regions, and are especially in the preponderance in temperate regions. They are herbs, shrubs, and trees, of every variety of size and habit, and the rich display of leaf forms is notably conspicuous.

Two great groups of Dicotyledons are recognized, the *Archichlamydeæ* and the *Sympetalæ*. In the former there is either no perianth or its parts are separate (polypetalous); in the latter the corolla is sympetalous. The Archichlamydeæ are the simpler forms, beginning in as simple a fashion as do the Monocotyledons; while the Sympetalæ

are evidently derived from them and become the most highly organized of all plants. The two groups each contain about forty thousand species, but the Archichlamydeæ contain about one hundred and sixty families, and the Sympetalæ about fifty.

To present over two hundred families, containing about eighty thousand species, is clearly impossible, and a very few of the prominent ones will be selected for illustrations.

Archichlamydeæ

138. **Poplars and their allies.**—This great alliance represents nearly five thousand species, and seems to form an isolated group. It is a notable tree assemblage, and apparently the most primitive and ancient group of Dicotyledons, containing the most important deciduous forest forms of

Fig. 238. An oak in winter condition.—From "Plant Relations."

temperate regions, for here belong the oak (Fig. 238), hickory, walnut, chestnut, beech, poplar, birch, elm (Figs. 198, 239), willow (Fig. 240), etc. The primitive character is indicated not merely by the floral structures, but also by the general anemophilous habit.

In the poplar (*Populus*) and its allied form, the willow (*Salix*), the flowers are naked and hypogynous (Fig. 196),

Fig. 239. An elm in foliage.—From "Plant Relations."

the stamens are indefinite in number (two to thirty), and the pistil is syncarpous (two carpels). The stamens and

Fig. 240. Flower clusters of willow (aments); that to the left is pistillate, the other staminate.—After Warming.

pistils are not only separated in different flowers, but upon different plants, some plants being staminate and others pistillate (Fig. 240). The flowers are clustered upon a long axis, and each one is protected by a prominent bract. It is these scaly bracts which give character to the cluster, which is called an *ament* or *catkin*, and the plants which produce such clusters are said to be *amentaceous*. These aments of poplars, "pussy willows," and the alders and birches are very familiar objects (Figs. 240, 241).

Fig. 241. Aments of alder (*Alnus*): *a*, branch with staminate aments (*n*), pistillate aments (*m*), and a young bud (*k*); *b*, pistillate ament at time of discharging seeds, showing the prominent bracts.—After Warming.

The only advanced character in the flowers as described above is the syncarpous pistil, but in the great allied pepper family (*Piperaceæ*) of the tropics, with its one thousand species, and most nearly represented in our flora by the

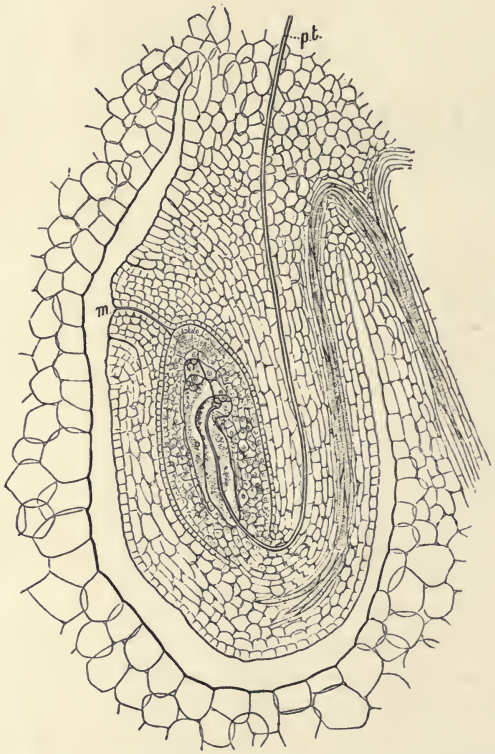


Fig. 242. Ovule of hornbeam (*Carpinus*), showing chalazogamy: *m*, the micropyle; *pt*, the pollen tube, which may be traced to its entrance into the embryo-sac at its antipodal end, and thence upward through the sac toward the egg.—After Mary Ewart.

lizard-tail (*Saururus*) of the swamps (Fig. 195), the flowers are not merely naked, but also apocarpous, and the whole structure is much like that of the simplest Monocotyle-

dons. The peppers seem to represent the simplest of the Dicotyledons, and this great line may have begun with some such forms.

A very interesting fact in connection with the fertilization of certain amentaceous plants has been discovered. In birch, alder, walnut, hornbeam, and some others, the pollen-tube does not enter the ovule by way of the micropyle, but pierces through in the region of the base of the ovule and so penetrates to the embryo-sac (Fig. 242). As the region of the ovule where integument and nucellus are not distinguishable is called the *chalaza*, this phenomenon is known as *chalazogamy*, meaning "fertilization through the chalaza."

139. **Buttercups and their allies.**—This is a great assemblage of terrestrial herbs, including nearly five thousand species, and is thought by many to be the great stock from which most of the higher Dicotyledons have been derived. The alliance includes the water-lilies, buttercups, and poppies, the specialized mustards, and certain notable tree forms, as magnolias, custard-apples, and the tropical laurels with one thousand species represented in our flora only by the sassafras. Here also is the strange group of "carnivorous" plants (*Sarracenia*, *Drosera*, *Dionæa*, etc.). The group is distinctly entomophilous, in striking contrast with the preceding one.

Taking the buttercup (*Ranunculus*) as a type (Fig. 202), the flower is hypogynous, the calyx and the corolla are distinctly differentiated and actinomorphic, and adapted for insect-pollination, but the spiral arrangement and indefinite numbers are very apparent, notably in connection with the apocarpous pistils, which are very numerous upon a prominent receptacle, but involving more or less all the parts. The stamens are also very numerous (Figs. 200, 243, 244). In the water-lilies the petals and stamens are indefinitely numerous (Fig. 203), and in the poppies there is no definite number. In many of the forms, however, in connection

Fig. 243. Marsh marigold (*Caltha*), a member of the Buttercup family, also showing floral diagram, in which the floral leaves are five, but the stamens and apocarpous pistils are indefinitely numerous.—After Atkinson.

Fig. 244. Zygomorphic flower of larkspur (*Delphinium*), with sepals removed, showing two petals with prominent spurs, and numerous stamens.—After Baillon.

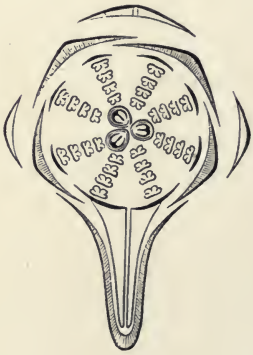


Fig. 245. Diagram of the zygomorphic flower of larkspur (*Delphinium*), showing the spur developed by a sepal and inclosing the two petal spurs.—After Baillon.

with one or more of the parts, the Dicotyl number (five) appears (Figs. 243, 245), but with no special constancy.

In certain genera of the buttercup family (*Ranunculaceæ*) zygomorphy appears, as in the larkspur (*Delphinium*) with its spurred petals and sepals (Figs. 244, 245), and the monkshood (*Aconitum*) with its hooded sepal; and in the

Fig. 246. The common cabbage (*Brassica*), a member of the mustard family: *A*, flower cluster, showing buds at tip, open flowers below with four spreading petals, and forming pods below; *B*, mature pod, with the persistent style; *C*, pod opening by two valves, and showing seeds attached to the false partition.—After Warming.

water-lily family (*Nymphæaceæ*) and poppy family (*Papaveraceæ*) syncarpy appears. In this alliance, also, belong the sweet-scented shrubs (*Calycanthus*), with their perigynous flowers containing numerous parts (Fig. 206).

The most specialized large group in this alliance is the mustard family (*Cruciferæ*), with twelve hundred species, to which belong the mustards, cresses, shepherd's purse, peppergrass, radish, cabbage (Fig. 246), etc. The sepals are four in two sets, the petals four in one set, the stamens six with two short ones in an outer set and four long ones in an inner set, and one carpel whose ovary becomes divided into two loculi by what is called a "false partition" (Figs. 246, *C*, 247), and usually becomes an elongated pod (Fig. 246, *A*, *B*). This specialized structure of the flower distinctly marks the family, whose name is suggested by the fact that the four spreading petals often form a Maltese cross (Fig. 246, *A*). The peculiar stamen character, four long and two short stamens, is called *tetradynamous* ("four strong").

Fig. 247. Diagram of crucifer flower, showing the relations of parts; four sepals, four petals, six stamens, and one carpel with a false partition. —After Warming.

140. **Roses.**—This family (*Rosaceæ*) of one thousand species is one of the best known and most useful groups of the temperate regions. In it are such forms as *Spiræa*, five-finger (*Potentilla*), strawberry (*Fragaria*) (Figs. 191, 207), raspberry (Fig. 248), and blackberry (*Rubus*), rose (*Rosa*), hawthorn (*Cratægus*), apple, and pear (*Pirus*) (Fig. 249), plum, cherry, almond, and peach (*Prunus*).

Fig. 248. The common raspberry: the figure to the left showing flower-stalk, calyx, old stamens (*s*), and prominent receptacle, from which the "fruit" (a cluster of small stone fruits, each representing a carpel) has been removed.—After Bailey.

Many of the true roses have a strong resemblance (Fig. 207) to the buttercups (*Ranunculus*), with their hypogynous regular flowers, and indefinite number of stamens and carpels, but the sepals and petals are much more frequently five, the Dicotyl number being better established. The

Fig. 249. The common pear (*Pirus communis*), showing branch with flowers (*1*), section of a flower (*2*) showing its epigynous character, section of fruit (*3*) showing the thickened calyx outside of the ovary or "core" (indicated by dotted outline), and flower diagram (*4*) showing all the organs in fives except the stamens.—After Wossidlo.

whole family remains actinomorphic, but perigyny and epigyny appear in certain forms (Fig. 205), giving rise to the peculiar fruit (*pome*) of apples and pears (Fig. 249), in which the calyx and ovary ripen together. Another specialized group of roses is that which develops the stone-

fruits (*drupes*), as apricots, peaches (Fig. 189), plums, cherries.

141. **Legumes.**—This is far the greatest family (*Leguminosæ*) of the Archichlamydeæ, containing about seven thousand species, distributed everywhere and of every habit. It is the great zygomorphic group of the Archichlamydeæ, being elaborately adapted to insect pollination. The more

Fig. 250. A legume plant (*Lotus*), showing flowering branch (*1*), a single flower (*2*) showing zygomorphic corolla, the cluster of ten stamens (*3*) which with the carpel is included in the keel, the solitary carpel (*4*) which develops into the pod or legume (*5*), the petals (*6*) dissected apart and showing standard (*a*), wings (*b*), and the two lower petals (*c*) which fold together to form the keel, and the floral diagram (*7*).—After Wossidlo.

primitive forms of the Leguminosæ, the mimosas, acacias (Fig. 251), etc., very much resemble true roses and the buttercups, with their hypogynous regular flowers and numerous stamens, but the vast majority are *Papilio* forms with very irregular (zygomorphic) flowers and few stamens

(Fig. 250). The petals are very dissimilar, the upper one (*standard*) being the largest, and erect or spreading, the two lateral ones (*wings*) oblique and descending, the two lower ones coherent by their edges to form a projecting boat-shaped body (*keel*), which incloses the stamens and pistil. From a fancied resemblance to a butterfly such flowers are said to be *papilionaceous*.

The whole family is further characterized by the single carpel, which after fertilization develops a pod (Fig. 250, *5*), which often becomes remarkably large as compared with the carpel. It is this peculiar pod (*legume*) which has given to the family its technical name *Leguminosæ* and the common name "Legumes."

FIG. 251. A sensitive-plant (*Acacia*), showing the flowers with inconspicuous petals and very numerous stamens, and the pinnately branched sensitive leaves.—After MEYER and SCHUMANN.

Well-known members of the family are lupine (*Lupinus*), clover (*Trifolium*), locust (*Robinia*), *Wistaria*, pea (*Pisum*), bean (*Phaseolus*), tragacanth (*Astragalus*), vetch (*Vicia*), redbud (*Cercis*), senna (*Cassia*), honey-locust (*Gleditschia*), indigo (*Indigofera*), sensitive-plants (*Acacia*, *Mimosa*, etc.) (Fig. 251), etc.

142. **Umbellifers.**—This is the most highly organized family (*Umbelliferæ*) of the Archichlamydeæ, which may be said to extend from Peppers to Umbellifers. The Legumes adopt zygomorphy, but remain hypogynous; and in some of the Roses epigyny appears; but the Umbellifers with their fifteen hundred species are all distinctly epigy-

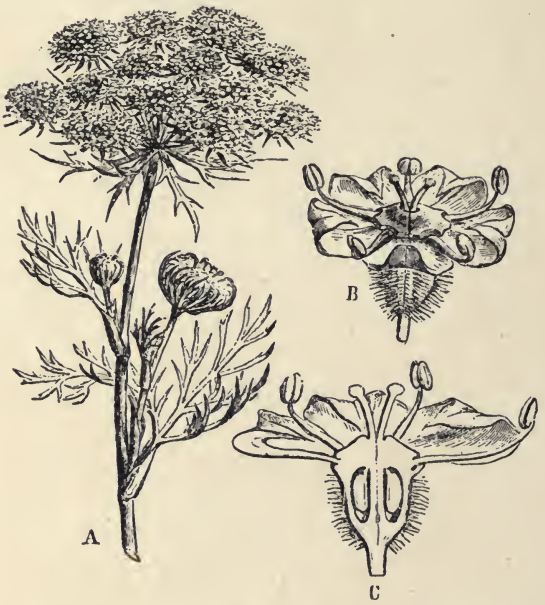


FIG. 252. The common carrot (*Daucus Carota*): *A*. branch bearing the compound umbels; *B*, a single epigynous flower, showing inferior ovary, five spreading petals, five stamens alternating with the petals, and the two styles of the bicarpellary pistil; *C*, section of flower, showing relation of parts, and also the minute sepals near the top of the ovary and just beneath the other parts.—After WARMING.

nous (Fig. 252, *B*, *C*), being one of the very few epigynous families among the Archichlamydeæ. In addition to epigyny, the cyclic arrangement and definite Dicotyl number is established, there being five sepals, five petals, five stamens, and two carpels, the highest known floral

formula, and one that appears among the highest Sympetalæ.

The name of the family is suggested by the characteristic inflorescence, which is also of advanced type. The flowers are reduced in size and massed in flat-topped clusters called *umbels* (Figs. 252, *A*, 253). The branches of the cluster arise in cycles from the axis like the braces of an umbrella. As a result of the close approximation of the flowers the sepals are much reduced in size and often obsolete (Fig. 252, *C*).

The Umbellifers are mainly perennial herbs of the north temperate regions, forming a very distinct family, and containing the following familiar forms: carrot (*Daucus*) (Fig. 252), parsnip (*Pastinaca*), hemlock (*Conium*) (Fig. 253), pepper-and-salt (*Erigenia*), caraway (*Carum*), fennel (*Fœniculum*), coriander (*Coriandrum*), celery (*Apium*), parsley (*Petroselinum*), etc. Allied to the Umbellifers are the Aralias (*Araliaceæ*), and the Dogwoods (*Cornaceæ*).

Fig. 253. Hemlock (*Conium*), an Umbellifer, showing the umbels, with the principal rays rising from a cycle of bracts (*involucre*), and each bearing at its summit a secondary umbel with its cycle of secondary bracts (*involucel*).—After Schimper.

Sympetalæ

143. **Introductory.**—These are the highest and the most recent Dicotyledons. While they contain numerous shrubs and trees in the tropics, they are by no means such a shrub and tree group in the temperate regions as are the Archichlamydeæ. The flowers are constantly cyclic, the number five or four is established, and the corolla is sympetalous, the stamens usually being borne upon its tube (Figs. 208, 209, 212).

There are two well-defined groups of Sympetalæ, distinguished from one another by the number of cycles and the number of carpels in the flower. The group containing the lower forms is *pentacyclic*, meaning "cycles five," there being two sets of stamens. In it also there are five carpels, the floral formula being, Sepals 5, Petals 5, Stamens 5 + 5, Carpels 5. As the carpels are the same in number as the other parts, the flowers are called *isocarpic*, meaning "carpels same." The group is named either *Pentacyclæ* or *Isocarpæ*, and contains about ten families and 4,000 species.

The higher groups, containing about forty families and 36,000 species, is *tetracyclic*, meaning "cycles four," and *anisocarpic*, meaning "carpels not the same," the floral formula being, Sepals 5, Petals 5, Stamens 5, Carpels 2. The group name, therefore, is *Tetracyclæ* or *Anisocarpæ*.

144. **Heaths.**—The Heath family (*Ericaceæ*) and its allies represent about two thousand species. They are mostly shrubs, sometimes trailing, and are displayed chiefly in temperate and arctic or alpine regions, in cold and damp or dry places, often being prominent vegetation in bogs and heaths, to which latter they give name (Fig. 254). The flowers are pentacyclic and isocarpic, as well as mostly hypogynous and actinomorphic. It is interesting to note that some forms are not sympetalous, the petals being distinct, showing a close relationship to the Archichlamydeæ. One of the marked characteristics of the group is the dehiscence

of the pollen-sacs by terminal pores, which are often prolonged into tubes (Fig. 255).

FIG. 254. Characteristic heath plants: *A*, *B*. *C*, *Lyonia*, showing sympetalous flowers and single style from the lobed syncarpous ovary; *D*, two forms of *Cassiope*, showing trailing habit, small overlapping leaves, and sympetalous flowers, but in the smaller form the petals are almost distinct.—After DRUDE.

Common representatives of the family are as follows: huckleberry (*Gaylussacia*), cranberry and blueberry (*Vaccinium*), bearberry (*Arctostaphylos*), trailing arbutus (*Epi-*

gœa), wintergreen (*Gaultheria*), heather (*Calluna*), mountain laurel (*Kalmia*), *Azalea*, *Rhododendron* (Fig. 256), Indian pipe (*Monotropa*), etc.

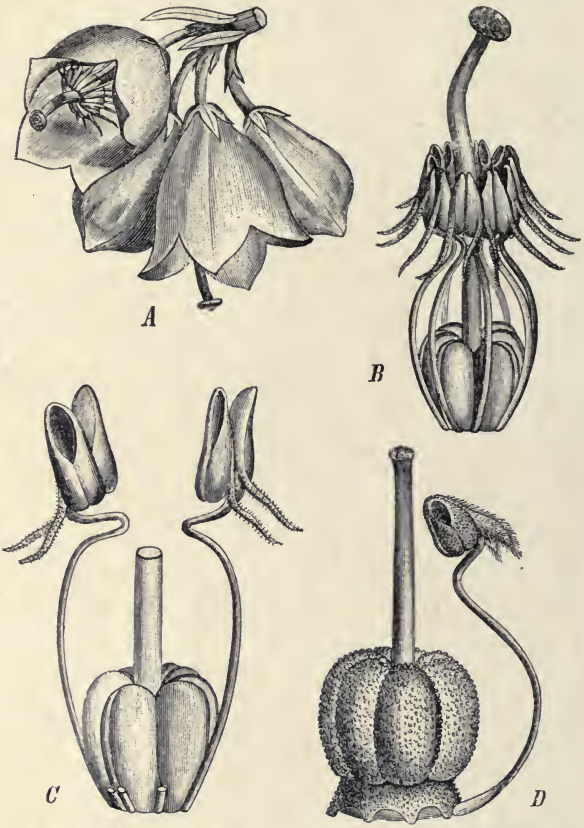


Fig. 255. Flowers of heath plants (*Erica*), showing complete flowers (*A*), the stamens with "two-horned" anthers which discharge pollen through terminal pores, and the lobed syncarpous ovary with single style and prominent terminal stigma (*B*, *C*, *D*).—After Drude.

145. **Convolvulus forms.**—The well-known morning-glory (*Ipomœa*) (Fig. 209) may be taken as a type of the Convol-

vulus family (*Convolvulaceæ*). Allied with it are *Polemonium* and *Phlox* (Fig. 210, *b*) (*Polemoniaceæ*), the gentians (*Gentianaceæ*), and the dog-banes (*Apocynaceæ*) (Fig. 257). It is here that the regular sympetalous flower reaches its highest expression in the form of conspicuous tubes, fun-

Fig. 256. A cluster of *Rhododendron* flowers.—After Hooker.

nels (Fig. 258), trumpets, etc. The flowers are tetracyclic and anisocarpic, besides being hypogynous and actinomorphic. These regular tubular forms represent about five thousand species, and contain many of the best-known flowers.

146. **Labiates.**—This great family (*Labiatæ*) and its alliances represent more than ten thousand species. The conspicuous feature is the zygomorphic flower, differing in this regard from the Convolvulus forms, which they resemble in being tetracyclic and anisocarpic, as well as hypogynous. The irregularity consists in organizing the mouth of the sympetalous corolla into two "lips," resulting in the *labiate* or

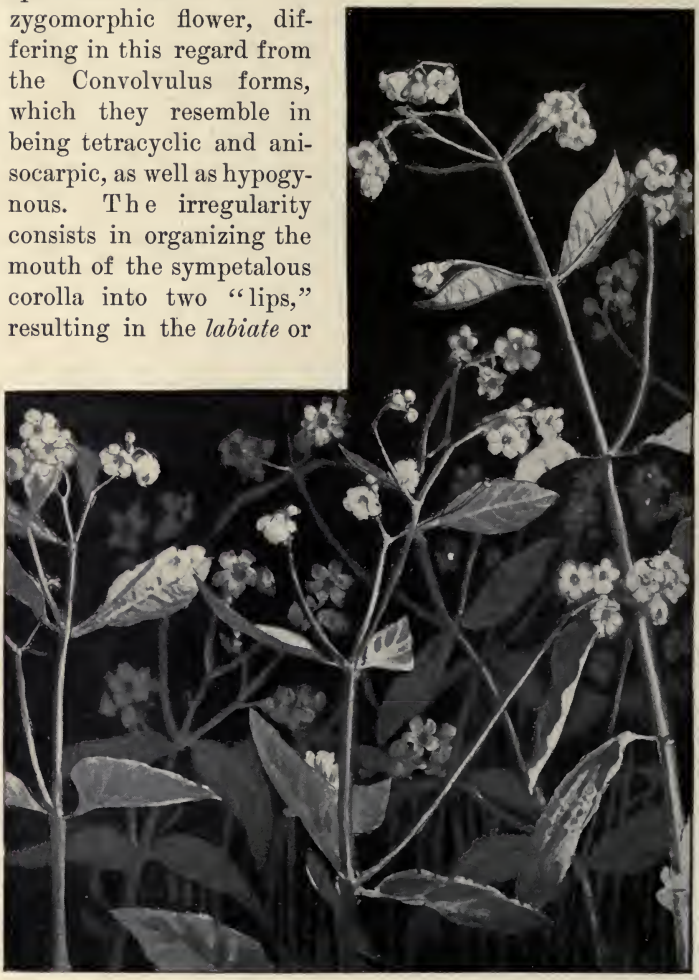


FIG. 257. A common dogbane (*Apocynum*).—From "Field, Forest, and Wayside Flowers."

FIG. 258. The hedge bindweed (*Convolvulus*), showing the twining habit and the conspicuous funnelform corollas.—From "Field, Forest, and Wayside Flowers."

bilabiate structure (Fig. 210, *c*, *d*, *e*), and suggesting the name of the dominant family. The upper lip usually contains two petals, and the lower three ; the two lips are sometimes widely separated, and sometimes in close contact, and differ widely in relative prominence.

Associated with zygomorphy in this group is a frequent reduction in the number of stamens, which are often four (Fig. 212) or two. The whole structure is highly specialized for the visits of insects, and this great zygomorphic alliance holds the same relative position among Sympetalæ as is held by the zygomorphic Legumes among Archichlamydeæ.

In the mint family, as the Labiates are often called, there are about two thousand seven hundred species, including mint (*Mentha*) (Fig. 212), dittany (*Cunila*), hyssop (*Hyssopus*), marjoram (*Origanum*),

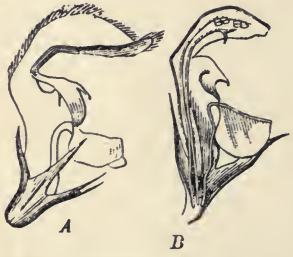


Fig. 259. Flowers of dead nettle (*Lamium*): *A*, entire bilabiate flower; *B*, section of flower, showing relation of parts.—After Warming.

Fig. 260. A labiate plant (*Teucrium*), showing branch with flower clusters (*A*), and side view of a few flowers (*B*), showing their bilabiate character.—After Briquet.

thyme (*Thymus*), balm (*Melissa*), sage (*Salvia*), catnip (*Nepeta*), skullcap (*Scutellaria*), horehound (*Marrubium*), lavender (*Lavandula*), rosemary (*Rosmarinus*), dead nettle (*Lamium*) (Fig. 259), *Teucrium* (Figs. 213, 260), etc., a remarkable series of aromatic forms.

Allied is the Nightshade family (*Solanaceæ*), with fifteen hundred species, containing such common forms as the nightshades and potato (*Solanum*), tomato (*Lycopersicum*), tobacco (*Nicotiana*) (Fig. 208), etc., in which the corolla is actinomorphic or nearly so; also the great Figwort family (*Scrophulariaceæ*), with two thousand species, represented by mullein (*Verbascum*), snapdragon (*Antirrhinum*) (Fig. 210, *e*), toad-flax (*Linaria*) (Fig. 210, *d*), *Pentstemon*, speedwell (*Veronica*), *Gerardia*, painted cup (*Castilleia*), etc.; also the Verbena family (*Verbenaceæ*), with over seven hundred species; and the two hundred plantains (*Plantaginaceæ*), etc.

147. **Composites.**—This greatest and ranking family (*Compositæ*) of Angiosperms is estimated to contain at least twelve thousand species, containing more than one seventh of all known Dicotyledons and more than one tenth of all Seed-plants. Not only is it the greatest family, but it is the youngest. Composites are distributed everywhere, but are most numerous in temperate regions, and are mostly herbs.

The name of the family suggests the most conspicuous feature—namely, the remarkably complete organization of the numerous small flowers into a compact head which resembles a single flower, formerly called a "compound flower." Taking the head of an *Arnica* as a type (Fig. 261), the outermost set of organs consists of more or less leaf-like bracts or scales (*involucre*), which resemble sepals; within these is a circle of flowers with conspicuous yellow corollas (*rays*), which are zygomorphic, being split above the tubular base and flattened into a strap-shaped body, and much resembling petals (Fig. 261, *A*, *D*); within the

FIG. 261. Flowers of *Arnica: A*, lower part of stem, and upper part bearing a head, in which are seen the conspicuous rays and the disk; *D*, single ray flower, showing the corolla, tubular at base and strap-shaped above, the two-parted style, the tuft of pappus hairs, and the inferior ovary which develops into a seed-like fruit (akene); *E*, single disk flower, showing tubular corolla with spreading limb, the two-parted style emerging from the top of the stamen tube, the prominent pappus, and the inferior ovary or akene; *C*, a single stamen.—After HOFFMAN.

ray-flowers is the broad expanse supplied by a very much broadened axis, and known as the *disk* (Fig. 261, *A*), which is closely packed with very numerous small and regular tubular flowers, known as *disk-flowers* (Fig. 261, *e*).

FIG. 262. The common dandelion (*Taraxacum*): *1*, two flower stalks; in one the head is closed, showing the double involucre, the inner erect, the outer reflexed, in the other the head open, showing that all the flowers are strap-shaped; *2*, a single flower showing inferior ovary, pappus, corolla, stamen tube, and two-parted style; *3*, a mature akene; *4*, a head from which all but one of the akenes have been removed, showing the pitted receptacle and the prominent pappus beak.—After STRASBURGER.

The division of labor among the flowers of a single head is plainly marked, and sometimes it becomes quite complex. The closely packed flowers have resulted in modifying the sepals extremely. Sometimes they disappear en-

tirely ; sometimes they become a tuft of delicate hairs, as in *Arnica* (Fig. 261, *D*, *E*), thistle (*Cnicus*), and dandelion (*Taraxacum*) (Fig. 263), surmounting the seed-like akene and aiding in its transportation through the air ; sometimes they are converted into two or more tooth-like and often

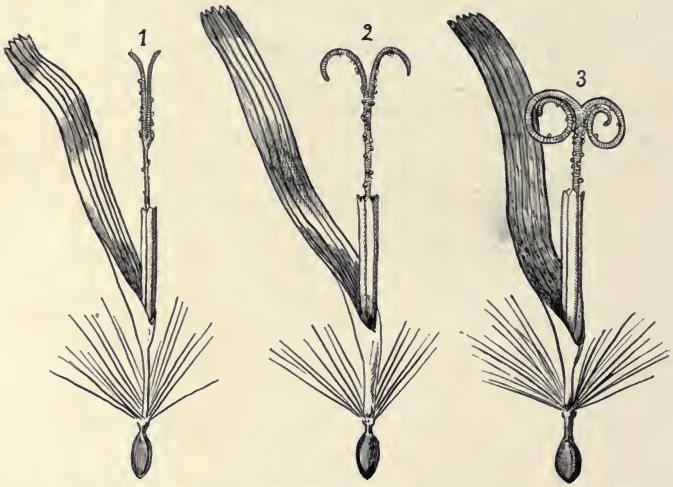


Fig. 263. Flowers of dandelion, showing action of style in removing pollen from the stamen tube: *1*, style having elongated through the tube and carrying pollen; *2*, style branches beginning to recurve; *3*, style branches completely recurved.— From "Field, Forest, and Wayside Flowers."

barbed processes arising from the akene, as in tickseed (*Coreopsis*) and beggar-ticks (Fig. 188) or Spanish needles (*Bidens*), to lay hold of passing animals ; sometimes they become beautifully plumose bristles, as in the blazing star (*Liatris*) ; sometimes they simply form a more or less conspicuous cup or set of scales crowning the akene. In all of these modifications the calyx is called *pappus*.

The stamens within the corolla are organized into a tube by their coalescent anthers (Fig. 263), and discharge their pollen within, which is carried to the surface of the

head and exposed by the swab-like rising of the style (Fig. 263). The head is thus smeared with pollen, and visiting insects can not fail to distribute it over the head or carry it to some other head.

In the dandelion and its allies the flowers of the disk are like the ray-flowers, the corolla being zygomorphic and strap-shaped (Figs. 262, 263).

The combination of characters is sympetalous, tetracyclic, and anisocarpic flowers, which are epigynous and often zygomorphic, with stamens organized into a tube and calyx modified into a pappus, and numerous flowers organized into a compact involucrate head in which there is more or less division of labor. There is no group of plants that shows such high organization, and the Compositæ seem to deserve the distinction of the highest family of the plant kingdom.

The well-known forms are too numerous to mention, but among them, in addition to those already mentioned, there are iron-weed (*Vernonia*), *Aster*, daisy (*Bellis*), goldenrod (*Solidago*), rosin-weed and compass-plant (*Silphium*), sunflower (*Helianthus*), *Chrysanthemum*, ragweed (*Ambrosia*), cocklebur (*Xanthium*), ox-eye daisy (*Leucanthemum*), tansy (*Tanacetum*), wormwood and sage-brush (*Artemisia*), lettuce (*Lactuca*), etc.

CHAPTER XV

DIFFERENTIATION OF TISSUES

148. **Introductory.**—Among the simplest Thallophytes the cells forming the body are practically all alike, both as to form and work. What one cell does all do, and there is very little dependence of cells upon one another. As plant bodies become larger this condition of things can not continue, as all of the cells can not be put into the same relations. In such a body certain cells can be related to the external food supply only through other cells, and the body becomes differentiated. In fact, the relating of cells to one another and to the external food-supply makes large bodies possible.

The first differentiation of the plant body is that which separates nutritive cells from reproductive cells, and this is accomplished quite completely among the Thallophytes. The differentiation of the tissues of the nutritive body, however, is that which specially concerns us in this chapter.

A tissue is an aggregation of similar cells doing similar work. Among the Thallophytes the nutritive body is practically one tissue, although in some of the larger Thallophytes the outer and the inner cells differ somewhat. This primitive tissue is composed of cells with thin walls and active protoplasm, and is called *parenchyma*, meaning "parent tissue."

Among the Bryophytes, in the leafy gametophore and in the sporogonium, there is often developed considerable dissimilarity among the cells forming the nutritive body, but the cells may all still be regarded as parenchyma. It

is in the sporophyte of the Pteridophytes and Spermatophytes that this differentiation of tissues becomes extreme, and tissues are organized which differ decidedly from parenchyma. This differentiation means division of labor, and the more highly organized the body the more tissues there are.

All the other tissues are derived from parenchyma, and as the work of nutrition and of reproduction is always retained by the parenchyma cells, the derived tissues are for mechanical rather than for vital purposes. There is a long list of these derived and mechanical tissues, some of them being of general occurrence, and others more restricted, and there is every gradation between them and the parenchyma from which they have come. We shall note only a few which are distinctly differentiated and which are common to all vascular plants.

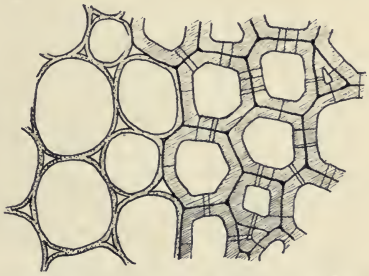


FIG. 264. Parenchyma and sclerenchyma from the stem of *Pteris*, in cross-section.—CHAMBERLAIN.

149. **Parenchyma.**—The parenchyma of the vascular plants is typically made up of cells which have thin walls and whose three dimensions are approximately equal (Figs. 264, 265), though sometimes they are elongated. Until abandoned, such cells contain very active protoplasm, and it is in them that nutritive work and cell division are carried on. So long as these cells retain the power of cell division the tissue is called *meristem*, or it is said to be *meristematic*, from a Greek word meaning "to divide." When the cells stop dividing, the tissue is said to be *permanent*. The growing points of organs, as stems, roots, and leaves, are composed of parenchyma which is meristematic (Figs. 266, 274), and meristem occurs wherever growth is going on.

150. **Mestome and stereome.**—When the plant body becomes complex a conductive system is necessary, so that the different regions of the body may be put into communication. The material absorbed by the roots must be carried to the leaves, and the food manufactured in the leaves must be carried to regions of growth and storage. This business of transportation is provided for by the specially organized vessels referred to in preceding chapters, and all conducting tissue, of whatever kind, is spoken of collectively as *mestome*.

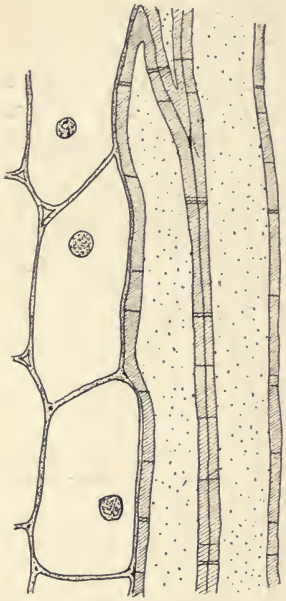


FIG. 265. Same tissues as in preceding figure, in longitudinal section, the parenchyma showing nuclei.—CHAMBERLAIN.

If a complex body is to maintain its form, and especially if it is to stand upright and become large, it must develop structures rigid enough to furnish mechanical support. All the tissues which serve this purpose are collectively known as *stereome*.

The sporophyte body of Pteridophytes and Spermatophytes, therefore, is mostly made up of living and working parenchyma, which is traversed by mechanical mestome and stereome.

151. **Dicotyl and Conifer stems.**—The stems of these two groups are so nearly alike in general plan that they may be considered together. In fact, the resemblances were once thought to be so important that these two groups were put together and kept distinct from Monocotyledons; but this was before the gametophyte structures were known to bear very different testimony.

At the apex of the growing stem there is a group of active meristem cells, from which all the tissues are derived (Fig. 266). This group is known as the *apical group*. Below the apical group the tissues and regions of the stem begin to appear, and still farther down they become distinctly differentiated, passing into permanent tissue, the apical group by its divisions continually adding to them and increasing the stem in length.

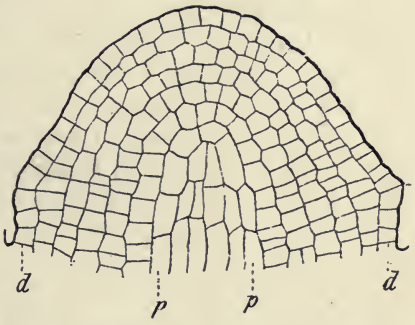


Fig. 266. Section through growing point of stem of *Hippuris*: below the growing point, composed of a uniform meristem tissue, the three embryonic regions are outlined, showing the dermatogen (*d*, *d*), the central plerome (*p*, *p*), and between them the periblem.—After De Bary.

Just behind the apical group, the cells begin to give the appearance of being organized into three great embryonic regions, the cells still remaining meristematic (Fig. 266). At the surface there is a single layer of cells distinct from those within, known as the *dermatogen*, or "skin-producer," as farther down, where it becomes permanent tissue, it is the *epidermis*. In the center of the embryonic region there is organized a solid cylinder of cells, distinct from those around it, and called the *plerome*, meaning "that which fills up." Farther down, where the plerome passes into permanent tissue, it is called the *central cylinder* or *stele* ("column"). Between the plerome and dermatogen is a tissue region called the *periblem*, meaning "that which is put around," and when it becomes permanent tissue it is called the *cortex*, meaning "bark" or "rind."

Putting these facts together, the general statement is that at the apex there is the apical group of meristem cells;

below them are the three embryonic regions, dermatogen, periblem, and plerome; and farther below these three regions pass into permanent tissue, organizing the epidermis, cortex, and stele. The three embryonic regions are usually not so distinct in the Conifer stem as in the Dicotyl stem, but both stems have epidermis, cortex, and stele.

Epidermis.—The epidermis is a protective layer, whose cells do not become so much modified but that they may be regarded as parenchyma. It gives rise also to superficial parts, as hairs, etc. In the case of trees, the epidermis does not usually keep up with the increasing diameter, and disappears. This puts the work of protection upon the cortex, which organizes a superficial tissue called *cork*, a prominent part of the structure known as *bark*.

Cortex.—The cortex is characterized by containing much active parenchyma, or primitive tissue, being the chief seat of the life activities of the stem. Its superficial cells, at least, contain chlorophyll and do chlorophyll work, while its deeper cells are usually temporary storage places for food. The cortex is also characterized by the development of stereome, or rigid tissues for mechanical support. The stereome may brace the epidermis, forming the *hypodermis;* or it may form bands and strands within the cortex; in fact, its amount and arrangement differ widely in different plants.

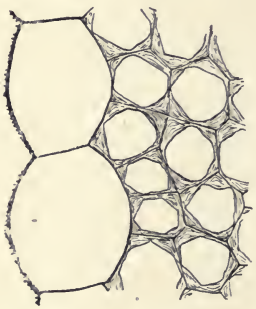


FIG. 267. Some collenchyma cells from the stem of a common dock (*Rumex*), showing the cells thickened at the angles.—CHAMBERLAIN.

The two principal stereome tissues are *collenchyma* and *sclerenchyma*, meaning "sheath-tissue" and "hard-tissue" respectively. In collenchyma the cells are thickened at the angles and have very elastic walls (Fig. 267), making the tissue well adapted for parts which are growing

in length. The chief mechanical tissue for parts which have stopped growing in length is sclerenchyma (Figs. 264, 265). The cells are thick-walled, and usually elongated and with tapering ends, including the so-called "fibers."

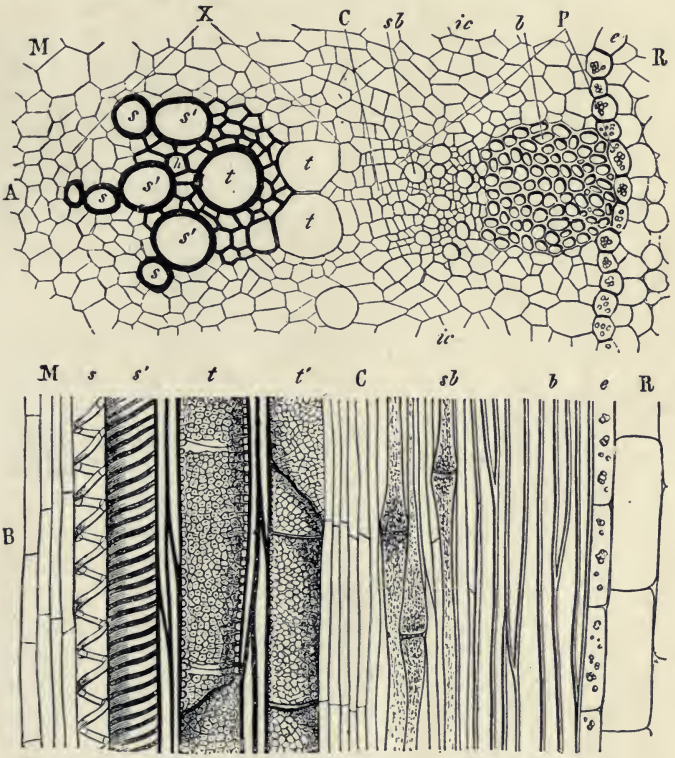


FIG. 268. Sections through an open collateral vascular bundle from a sunflower stem; *A*, cross-section; *B*, longitudinal section; the letters in both referring to the same structures; *M*, pith; *X*, xylem, containing spiral (*s*, *s'*) and pitted (*t*, *t'*) vessels; *C*, cambium; *P*, phloem, containing sieve vessels (*sb*); *b*, a mass of bast fibers or sclerenchyma; *ic*, pith rays between the bundles; *e*, the bundle sheath; *R*, cortex.—After VINES.

Stele.—The characteristic feature of the stele or central cylinder is the development of the mestome or vascular

tissues, of which there are two prominent kinds. The *tracheary vessels* are for water conduction, and are cells with heavy walls and usually large diameter (Fig. 268). The thickening of the walls is not uniform, giving them a very characteristic appearance, the thickening taking the form of spiral bands, rings, or reticulations (Fig. 268, *B*). Often the reticulation has such close meshes that the cell wall has the appearance of being covered with thin spots, and such cells are called "pitted vessels." The vessels with spirals and rings are usually much smaller in diameter than the pitted ones. The true tracheary cells are more or less elongated and without tapering ends, fitting end to end and forming a continuous longitudinal series, suggesting a trachea, and hence the name. In the Conifers there are no true tracheary cells, as in the Dicotyledons, except a few small spiral vessels which are formed at first in the young stele, but the tracheary tissue is made up of *tracheids*, meaning "trachea-like," differing from *tracheæ* or true tracheary vessels in having tapering ends and in not forming a continuous series (Fig. 269). The walls of these tracheids are "pitted" in a way which is characteristic of Gymnosperms, the "pits" appearing as two concentric rings, called "bordered pits."

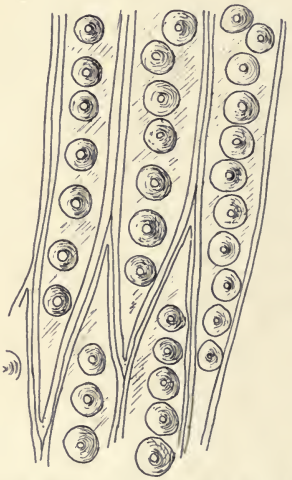


Fig. 269. Tracheids from wood of pine, showing tapering ends and bordered pits.—Chamberlain.

The other prominent mestome tissue developed in the stele is the *sieve vessels*, for the conduction of organized food, chiefly proteids (Fig. 268). Sieve cells are so named because in their walls special areas are organized which are perforated like the lid of a pepper-

box or a "sieve." These perforated areas are the *sieve-plates*, and through them the vessels communicate with one another and with the adjacent tissue.

The tracheary and sieve vessels occur in separate strands, the tracheary strand being called *xylem* ("wood"), the sieve strand *phloem* ("bark"). A xylem and a phloem strand are usually organized together to form a *vascular bundle*, and it is these fiber-like bundles which are found traversing the stems of all vascular plants and appearing conspicuously as the veins of leaves. Among the Dicotyls and Conifers the vascular bundles appear in the stele in such a way as to outline a hollow cylinder (Fig. 216), the xylem of each bundle being toward the center, the phloem toward the circumference of the stem. The undifferentiated parenchyma of the stele which the vascular cylinder incloses is called the *pith*. In older parts of the stem the pith is often abandoned by the activities of the plant, and either remains as a dead spongy tissue, or disappears entirely, leaving a hollow stem. Between the bundles forming the *vascular cylinder* there is also undifferentiated parenchyma, and as it seems to extend from the pith out between the bundles like "rays from the sun," the rays are called *pith rays*.

Such vascular bundles as described above, in which the xylem and phloem strands are "side-by-side" upon the same radius, are called *collateral* (Fig. 270). One of the peculiarities of the collateral bundles of Dicotyls and Conifers, however, is that when the two strands of each bundle are organized some meristem is left between them. This means that between the strands the work of forming new cells can go on. Such bundles are said to be *open;* and *the open collateral bundle* is characteristic of the stems of the Dicotyls and Conifers.

The meristem between the xylem and phloem of the open bundle is called *cambium* (Figs. 268, 270). The cambium also extends across the pith rays between the bundles,

connecting the cambium in the bundles, and thus forming a *cambium cylinder*, which separates the xylem and phloem of the vascular cylinder. This cambium continues the for-

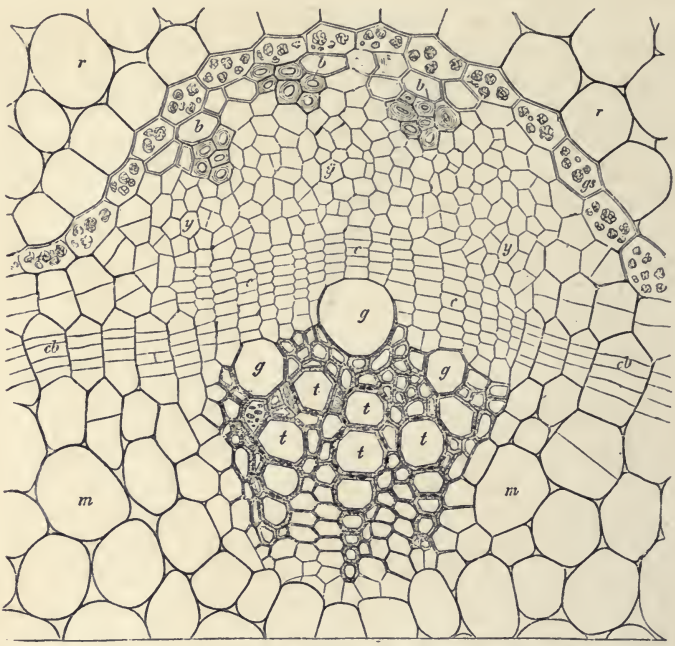


FIG. 270. Cross-section of open collateral vascular bundle from stem of castor-oil plant (*Ricinus*), showing pith cells (*m*), xylem containing spiral (*t*) and pitted (*g*) vessels, cambium of bundle (*c*) and of pith rays (*cb*), phloem containing sieve vessels (*y*), three bundles of bast fibers or sclerenchyma (*b*), the bundle sheath containing starch grains, and outside of it parenchyma of the cortex (*r*).—After SACHS.

mation of xylem tissue on the one side and phloem tissue on the other in the bundles, and new parenchyma between the bundles, and so the stem increases in diameter. If the stem lives from year to year the addition made by the cambium each season is marked off from that of the previous season, giving rise to the so-called *growth rings* or *annual rings*, so conspicuous a feature of the cross-section of tree

trunks (Fig. 217). This continuous addition to the vessels increases the capacity of the stem for conduction, and permits the further extension of branches and a larger display of leaves.

The annual additions to the xylem are added to the increasing mass of wood. The older portions of the xylem mass are gradually abandoned by the ascending water ("sap"), often change in color, and form the *heart-wood.* The younger portion, through which the sap is moving, is the *sap-wood.* It is evident, however, that the annual additions to the phloem are not in a position for permanency. The new phloem is deposited inside of the old, and this, together with the new xylem, presses upon the old phloem, which becomes ruptured in various ways, and rapidly or very gradually peels off, being constantly renewed from within. It is the protecting layers of cork (see this section under *Cortex*), the old phloem, and the new phloem down to the cambium, which constitute the so-called *bark* of trees, a structure exceedingly complex and extremely variable in different trees.

The stele also frequently develops stereome tissue in the form of sclerenchyma. These thick-walled fibers are often closely associated with one or both of the vascular strands of the bundles (Fig. 270), and lead to the old name *fibro-vascular bundles.*

To sum up, the stems of Dicotyledons and Conifers are characterized by the development of a vascular cylinder, in which the bundles are collateral and open, permitting increase in diameter, extension of the branch system, and a continuous increase in leaf display.

152. **Monocotyl stems.**—In the stems of Monocotyledons there is the same apical development and differentiation (Fig. 266). The characteristic difference from the Dicotyl and Conifer type, just described, is in connection with the development of the vascular bundles in the stele. Instead of outlining a hollow cylinder, the bundles are scattered

through the stele (Fig. 214). This lack of regularity would interfere with the organization of a cambium cylinder, and we find the bundles collateral but *closed*—that is, with no meristem left between the xylem and phloem (Fig. 271).

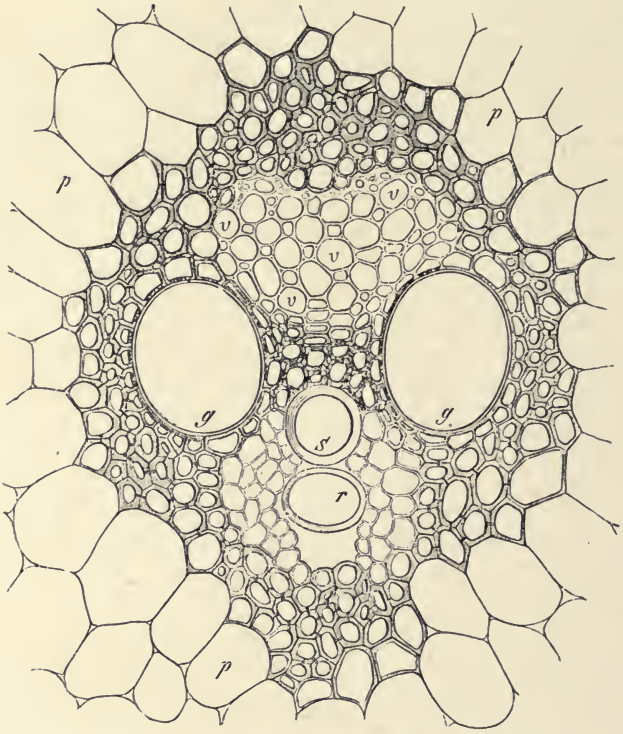


Fig. 271. Cross-section of a closed collateral bundle from the stem of corn, showing the xylem with annular (*r*), spiral (*s*), and pitted (*q*) vessels; the phloem containing sieve vessels (*v*), and separated from the xylem by no intervening cambium; both xylem and phloem surrounded by a mass of sclerenchyma (fibers); and investing vessels and fibers the parenchyma (*p*) of the pith-like tissue through which the bundles are distributed.—After Sachs.

This lack of cambium means that stems living for several years do not increase in diameter, but become columnar

shafts, as in the palm, rather than much elongated cones. It also means lack of ability to develop an extending branch system or to display more numerous leaves each year. The palm may be taken as a typical result of such a structure, with its columnar and unbranched trunk, and its foliage crown containing about the same number of leaves each year.

The lack of regular arrangement of the bundles also prevents the outlining of a pith region or the organization of definite pith rays. The failure to increase in diameter also precludes the necessity of bark, with its protective cork constantly renewed, and its sloughing-off phloem.

To sum up, the stems of the Monocotyledons are characterized by the vascular bundles not developing a cylinder or any regular arrangement, and by collateral and closed bundles, which do not permit increase in diameter, or a branch system, or increase in leaf display.

153. **Pteridophyte stems.**—The stems of Pteridophytes are quite different from those of Spermatophytes. While the large Club-mosses (*Lycopodium*) and *Isoetes* usually have an apical group of meristem cells, as among the Seed-plants, the smaller Club-mosses (*Selaginella*), Ferns, and Horsetails usually have a single apical cell, whose divisions give rise to all the cells of the stem. Generally also a dermatogen is not organized, and in such cases there is no true epidermis, the cortex developing the external protective tissue. In the cortex there is usually an extensive development of stereome, in the form of sclerenchyma (Fig. 272), the stele furnishing little or none, and the vascular bundles not adding much to the rigidity, as they do in the Seed-plants.

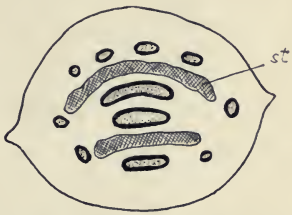


FIG. 272. Diagram of tissues in cross-section of stem of a fern (*Pteris*), showing two masses of sclerenchyma (*st*), between and about which are vascular bundles. — CHAMBERLAIN.

In *Equisetum* and *Isoetes* the vascular bundles may be said to be collateral, as in the Seed-plants, but the characteristic Pteridophyte type is very different. In fact, the vascular masses can hardly be compared with the bundles of the Seed-plants, although they are called bundles for convenience. In the stele one or more of these bundles are organized (Fig. 272), the tracheary vessels (xylem) being in the center and completely invested by the sieve vessels

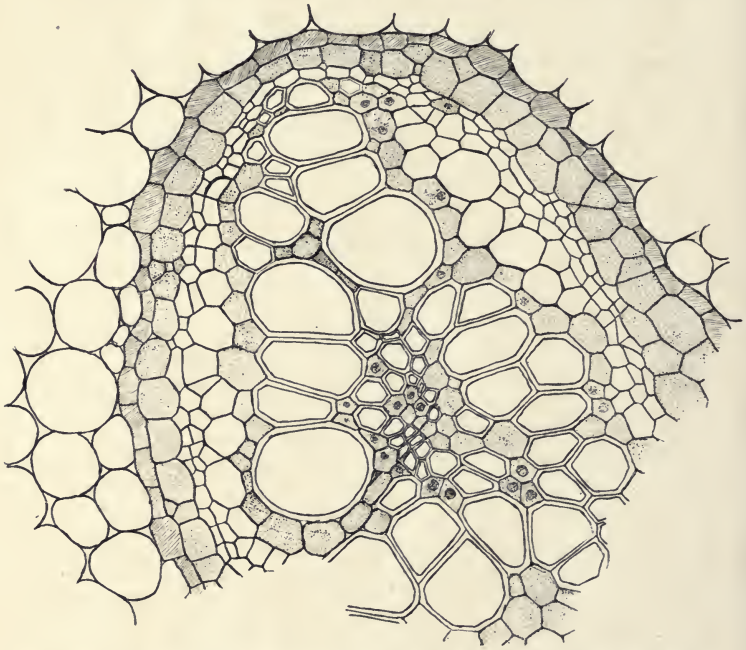


FIG. 273. Cross-section of concentric vascular bundle of a fern (*Pteris*): the single row of shaded cells investing the others is the bundle sheath; the large and heavy-walled cells within constitute the xylem; and between the xylem and the bundle sheath is the phloem.—CHAMBERLAIN.

(phloem). This is called the *concentric bundle* (Fig. 273), as distinguished from the collateral bundles of Seed-plants, and is characteristic of Pteridophyte stems.

154. **Roots.**—True roots appear only in connection with the vascular plants (Pteridophytes and Spermatophytes); and in all of them the structure is essentially the same, and quite different from stem structure. A single apical cell (in most Pteridophytes) (Fig. 274) or an apical group (in Spermatophytes) usually gives rise to the three embryonic regions — dermatogen, periblem, and plerome (Fig. 275).

A fourth region, however, peculiar to root, is usually added. The apical

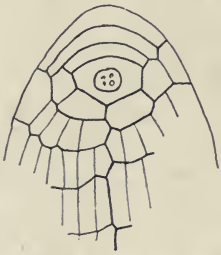


FIG. 274. Section through root-tip of *Pteris;* the cell with a nucleus is the single apical cell, which in front has cut off cells which organize the root-cap.—CHAMBERLAIN.

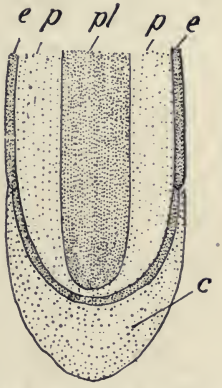


FIG. 275. A longitudinal section through the root-tip of shepherd's purse, showing the plerome (*pl*), surrounded by the periblem (*p*), outside of periblem the epidermis (*e*) which disappears in the older parts of the root, and the prominent root-cap (*c*). —From "Plant Relations."

cell or group cuts off a tissue in front of itself (Fig. 274), known as the *calyptrogen*, or "cap producer," for it organizes the *root-cap,* which protects the delicate meristem of the growing point.

Another striking feature is that in the stele there is organized a single solid vascular cylinder, forming a tough central axis (Fig. 277), from which the usually well-developed cortex can be peeled off as a thick rind. In this vascular axis, which is called "a bundle" for convenience but does not represent the bundle of Seed-plant stems, the arrangement of the xylem and phloem is entirely unlike that

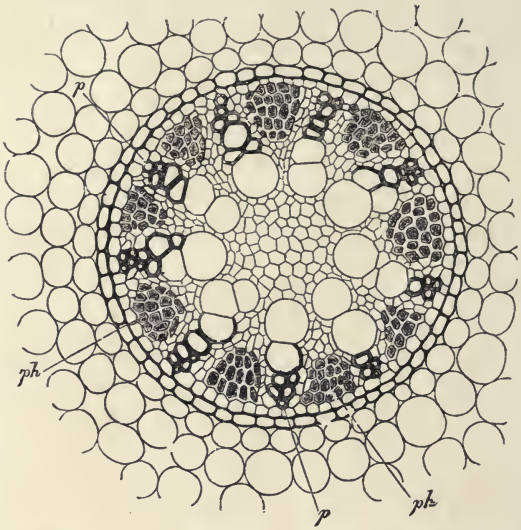


FIG. 276. Cross-section of the vascular axis of a root, showing radiate type of bundle the xylem (*p*) and phloem (*ph*) alternating.—After SACHS.

found in stems. The xylem is in the center and sends out a few radiating arms, between which are strands of phloem, forming the so-called *radiate bundle* (Fig. 276). This arrangement brings the tracheary vessels (xylem) to the surface of the bundle region, which is not true of either the concentric or collateral bundle. This seems to be associated with the fact that the xylem is to receive and conduct the water absorbed from the soil. It should be said that this characteristic

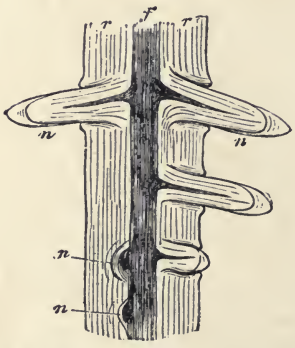


FIG. 277. Endogenous origin of root branches, showing them (*n*) arising from the central axis (*f*) and breaking through the cortex (*r*).—After VINES.

bundle structure of the root appears only in young and active roots. In older ones certain secondary changes take place which obscure the structure and result in a resemblance to the stem.

The origin of branches in roots is also peculiar. In stems branches originate at the surface, involving epidermis, cortex, and vascular bundles, such an origin being called *exogenous* ("produced outside"); but in roots branches originate on the vascular cylinder, burrow through the cortex, and emerge at the surface (Fig. 277). If the cortex be stripped off from a root with branches, the branches are left attached to the woody axis, and the cortex is found pierced with holes made by the burrowing branches. Such an origin is called *endogenous*, meaning "produced within."

To sum up the peculiarities of the root, it may be said to develop a root-cap, to have a solid vascular cylinder in which the xylem and phloem are arranged to form a bundle of the radiate type, and to branch endogenously.

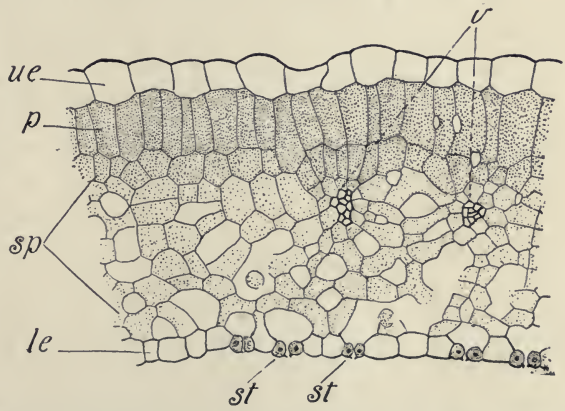


FIG. 278. A section through the leaf of lily, showing upper epidermis (*ue*), lower epidermis (*le*) with its stomata (*st*), mesophyll (dotted cells) composed of the palisade region (*p*) and the spongy region (*sp*) with air spaces among the cells, and two veins (*v*) cut across.—From "Plant Relations."

155. **Leaves.**—Leaves usually develop from an apical region in the same general way as do stems and roots, modified by their common dorsiventral character. Comparing the leaf of an ordinary seed-plant with its stem, it will be noted that the three regions are represented (Fig. 278): (1) the epidermis; (2) the cortex, represented by the mesophyll; (3) the stele, represented by the veins.

In the case of collateral bundles, where in the stem the xylem is always toward the center and the phloem is toward the circumference, in the leaves the xylem is toward the upper and the phloem toward the lower surface.

CHAPTER XVI

PLANT PHYSIOLOGY

156. **Introductory.**—Plants may be studied from several points of view, each of which has resulted in a distinct division of Botany. The study of the forms of plants and their structure is MORPHOLOGY, and it is this phase of Botany which has been chiefly considered in the previous chapters. The study of plants at work is PHYSIOLOGY, and as structure is simply preparation for work, the preceding chapters have contained some Physiology, chiefly in reference to nutrition and reproduction. The study of the classification of plants is TAXONOMY, and in the preceding pages the larger groups have been outlined. The study of plants as to their external relations is ECOLOGY, a subject which will be presented in the following chapter, and which is the chief subject of *Plant Relations*. The study of the diseases of plants and their remedies is PATHOLOGY; their study in relation to the interests of man is ECONOMIC BOTANY.

Besides these general subjects, which apply to all plants, the different groups form the subjects of special study. The study of the Morphology, Physiology, or Taxonomy of the Bacteria is *Bacteriology;* of the Algæ, *Algology;* of the Fungi, *Mycology;* of the Bryophytes, *Bryology;* of the fossil plants, *Palæobotany* or *Palæophytology*, etc.

In the present chapter it is the purpose to give a very brief outline of the great subject of Plant Physiology, not with the expectation of presenting its facts adequately, but with the hope that the important field thus presented may

attract to further study. It is merely the opening of a door to catch a fleeting glimpse.

A common division of the subject presents it under five heads: (1) Stability of form, (2) Nutrition, (3) Respiration, (4) Movement, (5) Reproduction.

STABILITY OF FORM

157. **Turgidity.**—It is a remarkable fact that plants and parts of plants composed entirely of cells with very thin and delicate walls are rigid enough to maintain their form. It has already been noted (see § 20) that such active cells exert an internal pressure upon their walls. This seems to be due to the active absorption of liquid, which causes the very elastic walls to stretch, as in the "blowing up" of a bladder. In this way each gorged and distended cell becomes comparatively rigid, and the mass of cells retains its form. It seems evident that the active protoplasm greedily pulls liquid through the wall and does not let it escape so easily. If for any reason the protoplasm of a gorged cell loses its hold upon the contained liquid the cell collapses.

158. **Tension of tissues.**—The rigidity which comes to active parenchyma cells through their turgidity is increased by the tensions developed by adjacent tissues. For example, the internal and external tissues of a stem are apt to increase in volume at different rates; the faster will pull upon the slower, and the slower will resist, and thus between the two a tension is developed which helps to keep them rigid. This is strikingly shown by splitting a dandelion stem, when the inner tissue, relieved somewhat from the resistance of the outer, elongates and causes the strip to become strongly curved outward or even coiled. Experiments with strips from active twigs, including the pith, will usually demonstrate the same curve outward. Tension of tissues is chiefly developed, of course, where elongation is taking place.

159. **Stereome.**—When growth is completed, cell walls lose their elasticity, turgidity becomes less, and therefore tensions diminish, and rigidity is supplied by special stereome tissues, chief among which is sclerenchyma. Another stereome tissue is collenchyma, which on account of its elastic walls can be used to supplement turgidity and tension where elongation is still going on. For a fuller account of stereome tissues see § 150.

NUTRITION

160. **Food.**—Plant food must contain carbon (C), hydrogen (H), oxygen (O), and nitrogen (N), and also more or less of other elements, notably sulphur, phosphorus, potassium, calcium, magnesium, and iron. In the case of green plants these elements are obtained from inorganic compounds and food is manufactured; while plants without chlorophyll obtain their food already organized. The sources of these elements for green plants are as follows: Carbon from carbon dioxide (CO_2) of the air; hydrogen and oxygen from water (H_2O); and nitrogen and the other elements from their various salts which occur in the soil and are dissolved in the water which enters the plant.

All of these substances must present themselves to plants in the form of a gas or a liquid, as they must pass through cell walls; and the processes of absorption have to do with the taking in of the gas carbon dioxide and of water in which the necessary salts are dissolved.

161. **Absorption.**—Green plants alone will be considered, as the unusual methods of securing food have been mentioned in Chapter VII. For convenience also, only terrestrial green plants will be referred to, as it is simple to modify the processes to the aquatic habit, where the surrounding water supplies what is obtained by land plants from both air and soil.

In such plants the carbon dioxide is absorbed directly from the air by the foliage leaves, whose expanse of surface is as important for this purpose as for exposing chlorophyll to light. When the work of foliage leaves is mentioned it must always be understood that it applies as well to any green tissue displayed by the plant.

The water, with its dissolved salts, is absorbed from the soil by the roots. Only the youngest parts of the root-system can absorb, and the absorbing capacity of these parts is usually vastly increased by the development of numerous *root hairs* just behind the growing tip (Fig. 194). These root hairs are ephemeral, new ones being continually put out as the tip advances, and the older ones disappearing. They come in very close contact with the soil particles, and "suck in" the water which invests each particle as a film.

162. **Transfer of water.**—The water and its dissolved salts absorbed by the root-system must be transferred to the foliage leaves, where they are to be used, along with the carbon dioxide, in the manufacture of food.

Having entered the epidermis of the absorbing rootlets the water passes on to the cortex, and traversing it enters the xylem system of the central axis. In some way this transfer is accompanied by pressure, known as *root pressure*, which becomes very evident when an active stem is cut off near the ground. The stump is said to "bleed," and sends out water ("sap") as if there were a force pump in the root-system. This root pressure doubtless helps to lift the water through the xylem of the root into the stem, and in low plants may possibly be able to send it to the leaves, but for most plants this is not possible.

When the water enters the xylem of the root it is in a continuous system of vessels which extends through the stem and out into the leaves. The movement of the absorbed water through the xylem is called the *transpiration current*, or very commonly the "ascent of sap." An ex-

periment demonstrating this ascent of sap and its route through the xylem will be found described in *Plant Relations*, p. 151. How it is that the transpiration current moves through the xylem is not certainly known.

163. **Transpiration.**—When the water carrying dissolved salts reaches the mesophyll cells, some of the water and all of the salts are retained for food manufacture. However, much more water enters the leaves than is needed for food, this excess having been used for carrying soil salts. When the soil salts have reached their destination the excess of water is evaporated from the leaf surface, the process being called *transpiration*. For an experiment demonstrating transpiration see *Plant Relations*, § 26.

This transpiration is regulated according to the needs of the plant. If the water is abundant, transpiration is encouraged; if the water supply is low, transpiration is checked. One of the chief ways of regulating is by means of the very small but exceedingly numerous stomata (see § 79 [4]), whose guard cells become turgid or collapse and so determine the size of the opening between them. It has been estimated that a leaf of an ordinary sunflower contains about thirteen million stomata, but the number varies widely in different plants. In ordinary dorsiventral leaves the stomata are much more abundant upon the lower surface than upon the upper, from which they may be lacking entirely. In erect leaves they are distributed equally upon both surfaces; in floating leaves they occur only upon the upper surface; in submerged leaves they are lacking entirely.

The amount of water thus evaporated from active leaves is very great. It is estimated that the leaves of a sunflower as high as a man evaporate about one quart of water in a warm day; and that an average oak tree in its five active months evaporates about twenty-eight thousand gallons. If these figures be applied to a meadow or a forest the result may indicate the large importance of this process.

164. **Photosynthesis.**—This is the process by which carbon dioxide and water are "broken up," their elements recombined to form a carbohydrate, and some oxygen given off as a waste product, the mechanism being the chloroplasts and light. It has been sufficiently described in § 55, and also in *Plant Relations*, pp. 28 and 150.

165. **Formation of proteids.**—The carbohydrates formed by photosynthesis, such as starch, sugar, etc., contain carbon, hydrogen, and oxygen. Out of them the living cells must organize proteids, and in the reconstruction nitrogen and sulphur, and sometimes phosphorus, are added. This work goes on both in green cells and other living cells, as it does not seem to be entirely dependent upon chloroplasts and light.

166. **Transfer of carbohydrates and proteids.**—These two forms of food having been manufactured, they must be carried to the regions of growth or storage. In order to be transported they must be in soluble form, and if not already soluble they must be *digested*, insoluble starch being converted into soluble sugar, etc. In these digested forms they are transported to regions where work is going on, and there they are *assimilated*—that is, transformed into the enormously complex working substance protoplasm; or they are transported to regions of storage and there they are reconverted into insoluble storage forms, as starch, etc.

These foods pass through both the cortex and phloem in every direction, but the long-distance transfer of proteids, as from leaves to roots, seems to be mainly through the sieve vessels.

RESPIRATION

167. **Respiration.**—This is an essential process in plants as well as in animals, and is really the phenomenon of "breathing." The external indication of the process is the absorption of oxygen and the giving out of carbon dioxide; and it goes on in all organs, day and night. When

it ceases death ensues sooner or later. By this process energy, stored up by the processes of nutrition, is liberated, and with this liberated energy the plant works. It may be said that oxygen seems to have the power of arousing protoplasm to activity.

It is not sufficient for the air containing oxygen to come in contact merely with the outer surface of a complex plant, as its absorption and transfer would be too slow. There must be an "internal atmosphere" in contact with the living cells. This is provided for by the intercellular spaces, which form a labyrinthine system of passageways, opening at the surface through stomata and *lenticels* (pores through bark). In this internal atmosphere the exchange of oxygen and carbon dioxide is effected, the oxygen being renewed by diffusion from the outside, and the carbon dioxide finally escaping by diffusion to the outside.

MOVEMENT

168. **Introductory.**—In addition to movements of material, as described above, plants execute movements dependent upon the activity of protoplasm, which result in change of position. Naked masses of protoplasm, as the plasmodium of slime-moulds (see § 51), advance with a sliding, snail-like movement upon surfaces; zoospores and ciliated sperms swim freely about by means of motile cilia; while many low plants, as Bacteria (§ 52), Diatoms (§ 34), *Oscillaria* (§ 20), etc., have the power of locomotion.

When the protoplasm is confined within rigid walls and tissues, as in most plants, the power of locomotion usually disappears, and the plants are fixed; but within active cells the protoplasm continues to move, streaming back and forth and about within the confines of the cell.

In the case of complex plants, however, another kind of movement is apparent, by which parts are moved and variously directed, sometimes slowly, sometimes with great

rapidity. In these cases the part concerned develops a curvature, and by various curvatures it attains its ultimate position. These curvatures are not necessarily permanent, for a perfectly straight stem results from a series of curvatures near its apex. Curvatures may be developed by unequal growth on the two sides of an organ, or by unequal turgidity of the cells of the two sides, or by the unequal power of the cell walls to absorb water.

169. **Hygroscopic movements.**—These movements are only exhibited by dry tissues, and hence are not the direct result of the activity of protoplasm. The dry walls absorb moisture and swell up, and if this absorption of moisture and its evaporation is unequal on two sides of an organ a curvature will result. In this way many seed vessels are ruptured, the sporangia of ferns are opened, the operculum of mosses is lifted off by the peristome, the hair-like pappus of certain Composites is spread or collapsed, certain seeds are dispersed and buried, etc. One of the peculiarities of this hygroscopic power of certain cells is that the result may be obtained through the absorption of the moisture of the air, and the hygroscopic awns of certain fruits have been used in the manufacture of rough hygrometers ("measures of moisture").

170. **Growth movements.**—Growth itself is a great physiological subject, but certain movements which accompany it are referred to here. Two kinds of growth movements are apparent.

One may be called *nutation*, by which is meant that the growing tip of an organ does not advance in a straight line, but bends now toward one side, now toward the other. In this way the tip describes a curve, which may be a circle, or an ellipse of varying breadth; but as the tip is advancing all the time, the real curve described is a spiral with circular or elliptical cross-section. The sweep of a young hop-vine in search of support, or of various tendrils, may be taken as extreme illustrations, but in most cases

the nutation of growing tips only becomes apparent through prolonged experiment.

The other prominent growth movement is that which places organs in proper relations for their work, sending roots into the soil and stems into the air, and directing leaf planes in various ways. For example, in the germination of an ordinary seed, in whatever direction the parts emerge the root curves toward the soil, the stem turns upward, and the cotyledons spread out horizontally.

The movement of nutation seems to be due largely to internal causes, while the movements which direct organs are due largely to external causes known as *stimuli*. Some of the prominent stimuli concerned in directing organs are as follows:

Heliotropism.—In this case the stimulus is light, and under its influence aërial parts are largely directed. Plants growing in a window furnish plain illustration of heliotropism. In general the stems and petioles curve toward the light, showing *positive heliotropism* (Fig. 279); the leaf blades are directed at right angles to the rays of light, showing *transverse heliotropism;* while if there are holdfasts or aërial roots they are directed away from the light, showing *negative heliotropism*. The thallus bodies of ferns, liverworts, etc., are transversely heliotropic, as ordinary leaves, a position best related to chlorophyll work. If the light is too intense, leaves may assume an edgewise or profile position, a condition well illustrated by the so-called "compass plants." (See *Plant Relations*, p. 10.)

Geotropism.—In this case the stimulus is gravity, and its influence in directing the parts of plants is very great. All upward growing plants, as ordinary stems, some leaves, etc., are *negatively geotropic*, growing away from the center of gravity. Tap-roots are notable illustrations of *positive geotropism*, growing toward the source of gravity with considerable force. Lateral branches from a main or tap-root, however, are usually *transversely geotropic*.

FIG. 279. Sunflower stems with the upper part of the stem sharply bent toward the light, giving the leaves better exposure, the stem showing positive heliotropism.—After SCHAFFNER.

That these influences in directing are very real is testified to by the fact that when the organs are turned aside from their proper direction they will curve toward it and overcome a good deal of resistance to regain it. Although these curvatures are mainly developed in growing parts, even mature parts which have been displaced may be brought back into position. For example, when the stems of certain plants, notably the grasses, have been prostrated by wind, etc., they often can resume the erect position under the influence of negative geotropism, a very strong and even angular curvature being developed at certain joints.

Hydrotropism.—The influence of moisture is very strong in directing certain organs, notably absorbing systems. Roots often wander widely and in every direction under the guidance of hydrotropism, even against the geotropic influence. Ordinarily geotropism and hydrotropism act in the same direction, but it is interesting to dissociate them so that they may "pull" against one another. For such an experiment see *Plant Relations*, p. 91.

Other stimuli.—Other outside stimuli which have a directive influence upon organs are chemical substances (*chemotropism*), such as direct sperms to the proper female organ ; heat (*thermotropism*) ; water currents (*rheotropism*) ; mechanical contact, etc. The most noteworthy illustrations of the effect of contact are furnished by tendril-climbers. When a nutating tendril comes in contact with a support a sharp curvature is developed which grasps it. In many cases the irritable response goes further, the tendril between the plant axis and the support developing a spiral coil.

171. **Irritable movements.**—The great majority of plants can execute movements only in connection with growth, as described in the preceding section, and when mature their parts are fixed and incapable of further adjustment. Certain plants, however, have developed the power of moving mature parts, the motile part always being a leaf, such as

foliage leaf, stamen, etc. It is interesting to note that these movements have been cultivated by but few families, notable among them being the Legumes (§ 141).

These movements of mature organs, some of which are very rapid, are due to changes in the turgidity of cells. As already mentioned (§ 157), turgid cells are inflated and rigid, and when turgidity ceases the cells collapse and the tissue becomes flaccid. A special organ for varying turgidity, known as the *pulvinus*, is usually associated with the motile leaves and leaflets. The pulvinus is practically a mass of parenchyma cells, whose turgidity is made to vary by various causes, and leaf-movement is the result.

The causes which induce some movements are unknown, as in the case of *Desmodium gyrans* (see *Plant Relations*, p. 49), whose small lateral leaflets uninterruptedly describe circles, completing a cycle in one to three minutes.

In other cases the inciting cause is the change from light to dark, the leaves assuming at night a very different position from that during the day. During the day the leaflets are spread out freely,

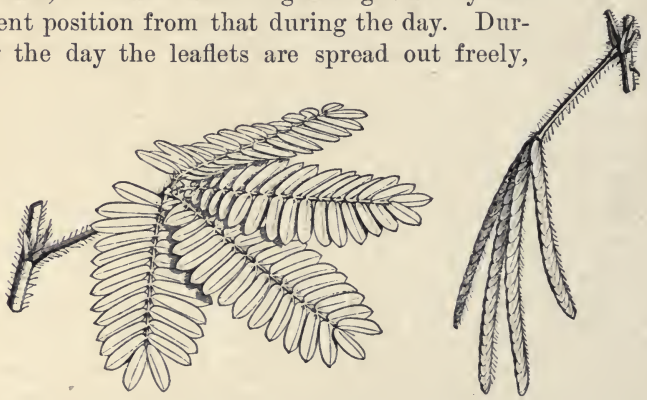


FIG. 280. A leaf of a sensitive plant in two conditions: in the figure to the left the leaf is fully expanded, with its four main divisions and numerous leaflets well spread; in the figure to the right is shown the same leaf after it has been "shocked" by a sudden touch, or by sudden heat, or in some other way; the leaflets have been thrown together forward and upward, the four main divisions have been moved together, and the main leaf-stalk has been directed sharply downward.—After DUCHARTRE.

while at night they droop and usually fold together (see *Plant Relations,* pp. 9, 10). These are the so-called *nyctitropic* movements or "night movements," which may be observed in many of the Legumes, as clover, locust, bean, etc.

In still other cases, mechanical irritation induces movement, as sudden contact, heat, injury, etc. Some of the "carnivorous plants" are notable illustrations of this, especially *Dionæa,* which snaps its leaves shut like a steel trap when touched (see *Plant Relations,* p. 161). Among the most irritable of plants are the so-called "sensitive plants," species of *Mimosa, Acacia,* etc., all of them Legumes. The most commonly cultivated sensitive plant is *Mimosa pudica* (Fig. 280), whose sensitiveness to contact and rapidity of response are remarkable (see *Plant Relations,* p. 48).

REPRODUCTION

172. **Reproduction.**—The important function of reproduction has been considered in connection with the various plant groups. Among the lowest plants the only method of reproduction is cell division, which in the complex forms results in growth. In the more complex plants various outgrowths or portions of the body, as gemmæ, buds, bulbs, tubers, various branch modifications, etc., furnish means of propagation. All of these methods are included under the head of *vegetative multiplication,* as the plants are propagated by ordinary vegetative tissues.

When a special cell is organized for reproduction, distinct from the vegetative cells, it is called a *spore,* and *reproduction by spores* is introduced. The first spores developed seem to have been those produced by the division of the contents of a mother cell, and are called *asexual spores.* These spores are scattered in various ways—by swimming (zoospores), by floating, by the wind, by insects.

Another type of spore is the *sexual spore,* formed by the union of two sexual cells called *gametes.* The gametes

seem to have been derived from asexual spores. At first the pairing gametes are alike, but later they become differentiated into *sperms* or male cells, and *eggs* or female cells.

With the establishment of alternation of generations, the asexual spores are restricted to the *sporophyte*, and the gametes to the *gametophyte*. With the further introduction of *heterospory*, the male and the female gametes are separated upon different gametophytes, which become much reduced.

With the reduction of the megaspores to one in a sporangium (ovule), and its retention, the *seed* is organized, and the elaborate scheme of insect-pollination is developed.

CHAPTER XVII

PLANT ECOLOGY

173. **Introductory.**—Ecology has to do with the external relations of plants, and forms the principal subject of the volume entitled *Plant Relations,* which should be consulted for fuller descriptions and illustrations. It treats of the adjustment of plants and their organs to their physical surroundings, and also their relations with one another and with animals, and has sometimes been called "plant sociology."

LIFE RELATIONS

174. **Foliage leaves.**—The life relation essential to foliage leaves is the relation to light. This is shown by their positions and forms, as well as by their behavior when deprived of light. This light relation suggests the answer to very many questions concerning leaves. It is not very important to know the names of different forms and different arrangements of leaves, but it is important to observe that these forms and arrangements are in response to the light relation.

In general a leaf adjusts its own position and its relation to its fellows so as to receive the greatest amount of light. Upon erect stems the leaves occur in vertical rows which are uniformly spaced about the circumference. If these rows are numerous the leaves are narrow; if they are few the leaves are usually broad. If broad leaves were associated with numerous rows there would be excessive shading;

if narrow leaves were associated with few rows there would be waste of space.

It is very common to observe the lower leaves of a stem long-petioled, those above short-petioled, and so on until the uppermost have sessile blades, thus thrusting the blades of lower leaves beyond the shadow of the upper leaves. There may also be a gradual change in the size and direction of the leaves, the lower ones being relatively large and horizontal, and the upper ones gradually smaller and more directed upward. In the case of branched (compound) leaves the reduction in the size of the upper leaves is not so necessary, as the light strikes between the upper leaflets and reaches those below.

On stems exposed to light only or chiefly on one side, the leaf blades are thrown to the lighted side in a variety of ways. In ivies, many prostrate stems, horizontal branches of trees, etc., the leaves brought to the lighted side are observed to form regular mosaics, each leaf interfering with its neighbor as little as possible.

There is often need of protection against too intense light, against chill, against rain, etc., which is provided for in a great variety of ways. Coverings of hairs or scales, the profile position, the temporary shifting of position, rolling up or folding, reduction in size, etc., are some of the common methods of protection.

175. **Shoots.**—The stem is an organ which is mostly related to the leaves it bears, the stem with its leaves being the *shoot*. In the foliage-bearing stems the leaves must be displayed to the light and air. Such stems may be subterranean, prostrate, floating, climbing, or erect, and all of these positions have their advantages and disadvantages, the erect type being the most favorable for foliage display.

In stems which bear scale leaves no light relation is necessary, so that such shoots may be and often are subterranean, and the leaves may overlap, as in scaly buds and bulbs. The subterranean position is very favorable

for food storage, and such shoots often become modified as food depositories, as in bulbs, tubers, rootstocks, etc. In the scaly buds the structure is used for protection rather than storage.

The stem bearing floral leaves is the shoot ordinarily called "the flower," whose structure and work have been sufficiently described. Its adjustments have in view pollination and seed dispersal, two very great ecological subjects full of interesting details.

176. **Roots.**—Roots are absorbent organs or holdfasts or both, and they enter into a variety of relations. Most common is the soil relation, and the energetic way in which such roots penetrate the soil, and search in every direction for water and absorb it, proves them to be highly organized members. Then there are roots related to free water, and others to air, each with its appropriate structure. More mechanical are the clinging roots (ivies, etc.), and prop roots (screw pines, banyans, etc.), but their adaptation to the peculiar service they render is none the less interesting.

The above statements concerning leaves, shoots, and roots should be applied with necessary modifications to the lower plants which do not produce such organs. The light relation and its demands are no less real among the Algæ than among Spermatophytes, as well as relations to air, soil, water, mechanical support, etc.

PLANT SOCIETIES

177. **Introductory.**—Plants are not scattered at haphazard over the surface of the earth, but are organized into definite communities. These communities are determined by the conditions of living—conditions which admit some plants and forbid others. Such an association of plants living together in similar conditions is a *plant society*. Closely related plants do not usually live together

in the same society, as their rivalry is too intense; but each society is usually made up of unrelated plants which can make use of the same conditions.

There are numerous factors which combine to determine societies, and it is known as yet only in a vague way how they operate.

178. **Ecological factors.**— *Water.*—This is a very important factor in the organization of societies, which are usually local associations. Taking plants altogether, the amount of water to which they are exposed varies from complete submergence to perpetual drought, but within this range plants vary widely as to the amount of water necessary for living.

Heat.—In considering the general distribution of plants over the surface of the earth, great zones of plants are outlined by zones of temperature; but in the organization of local societies in any given area the temperature conditions are nearly uniform. Usually plants work only at temperatures between 32° and 122° Fahr., but for each plant there is its own range of temperature, sometimes extensive, sometimes restricted. Even in plant societies, however, the effect of the heat factor may be noted in the succession of plants through the working season, spring plants being very different from summer and autumn plants.

Soil.—The great importance of this factor is evident, even in water plants, for the soil of the drainage area determines the materials carried by the water. Soil is to be considered both as to its chemical composition and its physical properties, the latter chiefly in reference to its disposition toward water. Soils vary greatly in the power of receiving and retaining water, sand having a high receptive and low retentive power, and clay just the reverse, and these factors have large effect upon vegetation.

Light.—All green plants can not receive the same amount of light. Hence some of them have learned to live with a

less amount than others, and are "shade plants" as distinct from "light plants." In forests and thickets many of these shade plants are to be seen, which would find an exposed situation hard to endure. In almost every society, therefore, plants are arranged in strata, dependent upon the amount of light they receive, and the number of these strata and the plants characterizing each stratum are important factors to note.

Wind.—This is an important factor in regions where there are strong prevailing winds. Wind has a drying effect and increases the transpiration of plants, tending to impoverish them in water. In such conditions only those plants can live which are well adapted to regulate transpiration.

The above five factors are among the most important, but no single factor determines a society. As each factor has a large possible range, the combinations of factors may be very numerous, and it is these combinations which determine societies. For convenience, however, societies are usually grouped on the basis of the water factor, at least three great groups being recognized.

179. **Hydrophyte societies.**—These are societies of water plants, the water factor being so conspicuous that the plants are either submerged or standing in water. A plant completely exposed to water, submerged, or floating, may be taken to illustrate the usual adaptations. The epidermal walls are thin, so that water may be absorbed through the whole surface; hence the root system is very commonly reduced or even wanting; and hence the water-conducting tissues (xylem) are feebly developed. The tissues for mechanical support (stereome) are feebly developed, the plant being sustained by the buoyant power of water. Such a plant, although maintaining its form in water, collapses upon removal. Very common also is the development of conspicuous air passages for internal aëration and for increasing buoyancy; and sometimes a special

buoyancy is provided for by the development of bladder-like floats.

Conspicuous among hydrophyte societies may be mentioned the following: (1) Free-swimming societies, in which the plants are entirely sustained by water, and are free to move either by locomotion or by water currents. Here belong the "plankton societies," consisting of minute plants and animals invisible to the naked eye, conspicuous among the plants being the diatoms; also the "pond societies," composed of algæ, duckweeds, etc., which float in stagnant or slow-moving waters.

(2) Pondweed societies, in which the plants are anchored, but their bodies are submerged or floating. Here belong the "rock societies," consisting of plants anchored to some firm support under water, the most conspicuous forms being the numerous fresh-water and marine algæ, among which there are often elaborate systems of holdfasts and floats. The "loose-soil societies" are distinguished by imbedding their roots or root-like processes in the mucky soil of the bottom (Figs. 281, 282). The water lilies with their broad floating leaves, the pondweeds or pickerel weeds with their narrow submerged leaves, are conspicuous illustrations, associated with which are algæ, mosses, water ferns, etc.

(3) Swamp societies, in which the plants are rooted in water, or in soil rich in water, but the leaf-bearing stems rise above the surface. The conspicuous swamp societies are "reed swamps," characterized by bulrushes, cat-tails and reed-grasses (Figs. 283, 284), tall wand-like Monocotyledons, usually forming a fringe about the shallow margins of small lakes and ponds; "swamp-moors," the ordinary swamps, marshes, bogs, etc., and dominated by coarse sedges and grasses (Fig. 282); "swamp-thickets," consisting of willows, alders, birches, etc.; "sphagnum-moors," in which sphagnummoss predominates, and is accompanied by numerous peculiar orchids, heaths, carnivorous plants, etc.;

FIG. 281.—A group of water plants (hydrophytes): in the foreground and to the right the yellow water poppy; to the left the water hyacinth; in the center water lilies.—CALDWELL.

FIG. 282. A series of plant societies, showing transition from hydrophyte to mesophyte societies as follows: lily pond, sedges at margin of water, grading into swamp grasses further back, then a shrub society, and in the background a tree society.—From photograph by W. L. LEWIS.

"swamp-forests," which are largely coniferous, tamarack (larch), pine, hemlock, etc., prevailing.

FIG. 283. Shore of Calumet Lake, Ill., showing the reed swamp growth of rushes and sedges.—COWLES.

180. **Xerophyte societies.**—These societies are exposed to the other extreme of the water factor, and are composed of plants adapted to dry air and soil. To meet these

drought conditions numerous adaptations have been developed and are very characteristic of xerophytic plants. Some of the conspicuous adaptations are as follows: peri-

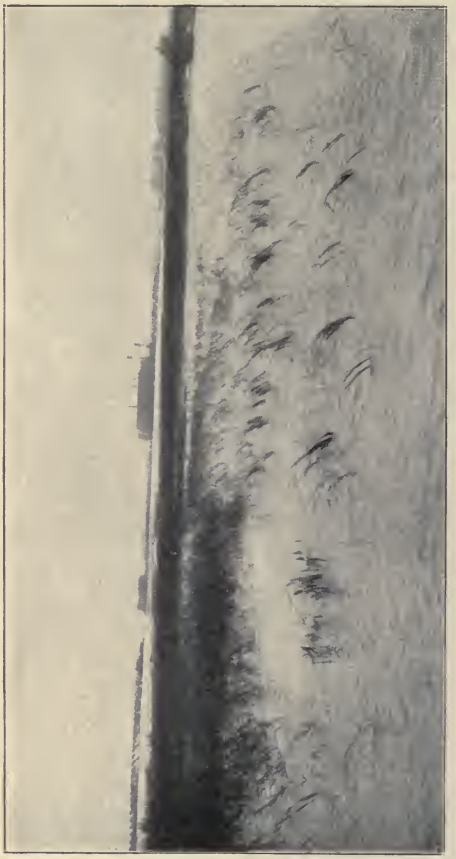


FIG. 284. The border of Lake Calumet, Ill., showing the advance of sedges and rushes into the deeper water, eventually leading to filling up.—COWLES.

odic reduction of surface, annuals bridging over a period of drought in the form of seeds, geophilous plants also disappearing from the surface and persisting in subterranean

Fig. 285. A shaded rock society near Utica, Ill. Under the overhanging ledges are various kinds of algæ, fungi, lichens, liverworts, mosses, ferns, and seed-plants.—Caldwell.

FIG. 286. "Starved Rock," on Illinois River near Utica, showing trees (mostly pines) growing in the rock crevices, along with other crevice plants forming a xerophyte rock society.—CALDWELL.

Fig. 287. A cliff society, composed chiefly of shrubs and trees. A white pine has sent roots over the edge of the cliff which have anchorage in the rock crevices.—Cowles and Caldwell.

parts, deciduous trees and shrubs dropping their leaves, etc.; temporary reduction of surface, the leaves rolling up or folding together in various ways; profile position, the leaves standing edgewise and not exposing their flat surfaces to the most intense light; motile leaves which can shift their position to suit their needs; small leaves, a very characteristic feature of xerophytic plants; coverings of hair; dwarf growth; anatomical adaptations, such as cuticle, palisade tissue, etc. Probably the most conspicuous adaptation, however, is the organization of "water-reservoirs," which collect and retain the scanty water supply, doling it out as the plant needs it.

Some of the prominent societies are as follows: "rock-societies" composed of plants living upon exposed rock surfaces, walls, fences, etc., notably lichens and mosses; "sand societies," including beaches, dunes, and sandy fields; "shrubby heaths," characterized by heath plants; "plains," the great areas of dry air and wind developed in the interiors of continents; "cactus deserts," still more arid areas of the Mexican region, where the cactus, agave, yucca, etc., have learned to live by means of the most extreme xerophytic modifications; "tropical deserts," where xerophytic conditions reach their extreme in the combination of maximum heat and minimum water; "xerophyte thickets," the most impenetrable of all thicket-growths, represented by the "chaparral" of the Southwest, and the "bush" and "scrub" of Africa and Australia; "xerophyte forests," also notably coniferous. (See Figs. 285, 286, 287.)

181. **Mesophyte societies.**—Mesophytes make up the common vegetation, the conditions of moisture being medium, and the soil fertile. This is the normal plant condition, and is the arable condition—that is, best adapted for the plants which man seeks to cultivate. If a hydrophytic area is to be cultivated, it is drained and made mesophytic; if a xerophytic area is to be cultivated, it is irrigated and

FIG. 288. A notable "dripping rock" society near La Salle, Ill., in which are numerous genera of lichens, liverworts, mosses, ferns, and seed-plants.—CALDWELL.

FIG. 289. A society of shrubs and trees whose roots prevent the washing away of the soil by the current, and so maintain an island. In the Illinois River, near "Starved Rock."—COWLES and CALDWELL.

made mesophytic. As contrasted with hydrophyte and xerophyte societies, the mesophyte societies are far richer in leaf forms and in general luxuriance. The artificial societies which have been formed under the influence of man, through the introduction of weeds and culture plants, are all mesophytic.

Among the mesophyte grass and herb societies are the "arctic and alpine carpets," so characteristic of high latitudes and altitudes where the conditions forbid trees, shrubs, or even tall herbs; "meadows," areas dominated by grasses, the prairies being the greatest meadows, where grasses and flowering herbs are richly displayed; "pastures," drier and more open than meadows.

Among the woody mesophyte societies are the "thickets," composed of willow, alder, birch, hazel, etc., either pure or forming a jungle of mixed shrubs, brambles, and tall herbs; "deciduous forests," the glory of the temperate regions, rich in forms and foliage display, with annual fall of leaves, and exhibiting the remarkable and conspicuous phenomenon of autumnal coloration; "rainy tropical forests," in the region of trade winds, heavy rainfalls, and great heat, where the world's vegetation reaches its climax, and where in a saturated atmosphere gigantic jungles are developed, composed of trees of various heights, shrubs of all sizes, tall and low herbs, all bound together in an inextricable tangle by great vines or lianas, and covered by a luxuriant growth of numerous epiphytes. (See Figs. 288, 289.)

GLOSSARY

[The definitions of a glossary are often unsatisfactory. It is much better to consult the fuller explanations of the text by means of the index. The following glossary includes only frequently recurring technical terms. Those which are found only in reasonably close association with their explanation are omitted. The number following each definition refers to the page where the term will be found most fully defined.]

ACTINOMORPHIC: applied to a flower in which the parts in each set are similar; regular. 228.

AKENE: a one-seeded fruit which ripens dry and seed-like. 212.

ALTERNATION OF GENERATIONS: the alternation of gametophyte and sporophyte in a life history. 94.

ANEMOPHILOUS: applied to flowers or plants which use the wind as agent of pollination. 181.

ANISOCARPIC: applied to a flower whose carpels are fewer than the other floral organs. 268.

ANTHER: the sporangium-bearing part of a stamen. 197.

ANTHERIDIUM: the male organ, producing sperms. 16.

ANTIPODAL CELLS: in Angiosperms the cells of the female gametophyte at the opposite end of the embryo-sac from the egg-apparatus. 205.

APETALOUS: applied to a flower with no petals. 221.

APOCARPOUS: applied to a flower whose carpels are free from one another. 226.

ARCHEGONIUM: the female, egg-producing organ of Bryophytes, Pteridophytes, and Gymnosperms. 100.

ARCHESPORIUM: the first cell or group of cells in the spore-producing series. 102.

ASCOCARP: a special case containing asci. 58.

ASCOSPORE: a spore formed within an ascus. 59.

ASCUS: a delicate sac (mother-cell) within which ascospores develop. 59.

ASEXUAL SPORE: one produced usually by cell-division, at least not by cell-union. 9.

CALYX : the outer set of floral leaves. 221.

CAPSULE : in Bryophytes the spore-vessel ; in Angiosperms a dry fruit which opens to discharge its seeds. 98, 211.

CARPEL : the megasporophyll of Spermatophytes. 178.

CHLOROPHYLL : the green coloring matter of plants. 5.

CHLOROPLAST : the protoplasmic body within the cell which is stained green by chlorophyll. 7.

COLUMELLA : in Bryophytes the sterile tissue of the sporogonium which is surrounded by the sporogenous tissue. 106.

CONIDIUM : an asexual spore formed by cutting off the tip of the sporophore, or by the division of hyphæ. 58.

CONJUGATION : the union of similar gametes. 15.

COROLLA : the inner set of floral leaves. 221.

COTYLEDON : the first leaf developed by an embryo sporophyte. 138.

CYCLIC : applied to an arrangement of leaves or floral parts in which two or more appear upon the axis at the same level, forming a cycle, or whorl, or verticil. 159.

DEHISCENCE : the opening of an organ to discharge its contents, as in sporangia, pollen-sacs, capsules, etc. 199.

DICHOTOMOUS : applied to a style of branching in which the tip of the axis forks. 35.

DIŒCIOUS : applied to plants in which the two sex-organs are upon different individuals. 115.

DORSIVENTRAL : applied to a body whose two surfaces are differently exposed, as an ordinary thallus or leaf. 109.

EGG : the female gamete. 16.

EGG-APPARATUS : in Angiosperms the group of three cells in the embryo-sac composed of the egg and the two synergids. 204.

ELATER : in Liverworts a spore-mother-cell peculiarly modified to aid in scattering the spores. 103.

EMBRYO : a plant in the earliest stages of its development from the spore. 137.

EMBRYO-SAC : the megaspore of Spermatophytes, which later contains the embryo. 178.

ENDOSPERM : the nourishing tissue developed within the embryo-sac, and thought to represent the female gametophyte. 180.

ENDOSPERM NUCLEUS : the nucleus of the embryo-sac which gives rise to the endosperm. 205.

ENTOMOPHILOUS : applied to flowers or plants which use insects as agents of pollination. 196.

EPIGYNOUS: applied to a flower whose outer parts appear to arise from the top of the ovary. 225.

EUSPORANGIATE: applied to those Pteridophytes and Spermatophytes whose sporangia develop from a group of epidermal and deeper cells. 157.

FAMILY: a group of related plants, usually comprising several genera. 236.

FERTILIZATION: the union of sperm and egg. 16.

FILAMENT: the stalk-like part of a stamen. 197.

FISSION: cell-division which includes the wall of the old cell. 10.

FOOT: in Bryophytes the part of the sporogonium imbedded in the gametophore; in Pteridophytes an organ of the sporophyte embryo to absorb from the gametophyte. 98, 138.

GAMETANGIUM: the organ within which gametes are produced. 11.

GAMETE: a sexual cell, which by union with another produces a sexual spore. 10.

GAMETOPHORE: a special branch which bears sex organs. 98.

GAMETOPHYTE: in alternation of generations, the generation which bears the sex organs. 97.

GENERATIVE CELL: in Spermatophytes the cell of the male gametophyte (within the pollen grain) which gives rise to the male cells. 180.

GENUS: a group of very closely related plants, usually comprising several species. 237.

HAUSTORIUM: a special organ of a parasite (usually a fungus) for absorption. 50.

HETEROGAMOUS: applied to plants whose pairing gametes are unlike. 15.

HETEROSPOROUS: applied to those higher plants whose sporophyte produces two forms of asexual spores. 151.

HOMOSPOROUS: applied to those plants whose sporophyte produces similar asexual spores. 151.

HOST: a plant or animal attacked by a parasite. 48.

HYPHA: an individual filament of a mycelium. 49.

HYPOCOTYL: the axis of the embryo sporophyte between the root-tip and the cotyledons. 209.

HYPOGYNOUS: applied to a flower whose outer parts arise from beneath the ovary. 224.

Indusium : in Ferns a flap-like membrane protecting a sorus. 143.
Inflorescence : a flower-cluster. 230.
Insertion : the point of origin of an organ. 224.
Integument : in Spermatophytes a membrane investing the nucellus. 178.
Involucre : a cycle or rosette of bracts beneath a flower-cluster, as in Umbellifers and Composites. 275.
Isocarpic : applied to a flower whose carpels equal in number the other floral organs. 268.
Isogamous : applied to plants whose pairing gametes are similar. 15.

Leptosporangiate : applied to those Ferns whose sporangia develop from a single epidermal cell. 157.

Male cell : in Spermatophytes the fertilizing cell conducted by the pollen-tube to the egg. 180.
Megasporangium : a sporangium which produces only megaspores. 152.
Megaspore : in heterosporous plants the large spore which produces a female gametophyte. 152.
Megasporophyll : a sporophyll which produces only megasporangia. 152.
Mesophyll : the tissue of a leaf between the two epidermal layers which usually contains chloroplasts. 141.
Microsporangium : a sporangium which produces only microspores. 152.
Microspore : in heterosporous plants the small spore which produces a male gametophyte. 152.
Microsporophyll : a sporophyll which produces only microsporangia. 152.
Micropyle : the passageway to the nucellus left by the integument. 178.
Monœcious : applied to plants in which the two sex organs are upon the same individual. 115.
Monopodial : applied to a style of branching in which the branches arise from the side of the axis. 35.
Mother cell : usually a cell which produces new cells by internal division. 9.
Mycelium : the mat of filaments which composes the working body of a fungus. 49.

Naked flower : one with no floral leaves. 222.
Nucellus : the main body of the ovule. 178.

Oogonium : the female, egg-producing organ of Thallophytes. 16.
Oosphere : the female gamete, or egg. 16.
Oospore : the sexual spore resulting from fertilization. 16.
Ovary : in Angiosperms the bulbous part of the pistil, which contains the ovules. 199.
Ovule : the megasporangium of Spermatophytes. 178.

Pappus : the modified calyx of the Composites. 278.
Parasite : a plant which obtains food by attacking living plants or animals. 48.
Pentacyclic : applied to a flower whose four floral organs are in five cycles, the stamens being in two cycles. 268.
Perianth : the set of floral leaves when not differentiated into calyx and corolla. 221.
Perigynous : applied to a flower whose outer parts arise from a cup surrounding the ovary. 225.
Petal : one of the floral leaves which make up the corolla. 221.
Photosynthesis : the process by which chloroplasts, aided by light, manufacture carbohydrates from carbon dioxide and water. 84.
Pistil : the central organ of the flower, composed of one or more carpels. 200.
Pistillate : applied to flowers with carpels but no stamens. 218.
Pollen : the microspores of Spermatophytes. 174.
Pollen-tube : the tube developed from the wall of the pollen grain which penetrates to the egg and conducts the male cells. 180.
Pollination : the transfer of pollen from anther to ovule (in Gymnosperms) or stigma (in Angiosperms). 181.
Polypetalous : applied to flowers whose petals are free from one another. 227.
Prothallium : the gametophyte of Ferns. 130.
Protonema : the thallus portion of the gametophyte of Mosses. 98.

Radial : applied to a body with uniform exposure of surface, and producing similar organs about a common center. 120.
Receptacle : in Angiosperms that part of the stem which is more or less modified to support the parts of the flower. 222.
Rhizoid : a hair-like process developed by the lower plants and by independent gametophytes to act as a holdfast or absorbing organ, or both. 109.

Saprophyte : a plant which obtains food from the dead bodies or body products of plants or animals. 48.

SCALE: a leaf without chlorophyll, and usually reduced in size. 161.

SEPAL: one of the floral leaves which make up the calyx. 221.

SETA: in Bryophytes the stalk-like portion of the sporogonium. 98.

SEXUAL SPORE: one produced by the union of gametes. 10.

SPECIES: plants so nearly alike that they all might have come from a single parent. 237.

SPERM: the male gamete. 16.

SPIRAL: applied to an arrangement of leaves or floral parts in which no two appear upon the axis at the same level; often called alternate. 193.

SPORANGIUM: the organ within which asexual spores are produced (except in Bryophytes). 10.

SPORE: a cell set apart for reproduction. 9.

SPOROGONIUM: the leafless sporophyte of Bryophytes. 98.

SPOROPHORE: a special branch bearing asexual spores. 49.

SPOROPHYLL: a leaf set apart to produce sporangia. 145.

SPOROPHYTE: in alternation of generations, the generation which produces the asexual spores. 97.

STAMEN: the microsporophyll of Spermatophytes. 174.

STAMINATE: applied to a flower with stamens but no carpels. 218.

STIGMA: in Angiosperms that portion of the carpel (usually of the style) prepared to receive pollen. 199.

STOMA (pl. STOMATA): an epidermal organ for regulating the communication between green tissue and the air. 141.

STROBILUS: a cone-like cluster of sporophylls. 161.

STYLE: the stalk-like prolongation from the ovary which bears the stigma. 199.

SUSPENSOR: in heterosporous plants an organ of the sporophyte embryo which places it in a more favorable position in reference to food supply. 168.

SYMBIONT: an organism which enters into the condition of symbiosis. 79.

SYMBIOSIS: usually applied to the condition in which two different organisms live together in intimate and mutually helpful relations. 79.

SYMPETALOUS: applied to a flower whose petals have coalesced. 227.

SYNCARPOUS: applied to a flower whose carpels have coalesced. 226.

SYNERGID: in Angiosperms one of the pair of cells associated with the egg to form the egg-apparatus. 204.

Testa : the hard coat of the seed. 184.

Tetracyclic : applied to a flower whose four floral organs are in four cycles. 268.

Tetrad : a group of four spores produced by a mother-cell. 103.

Zoospore : a motile asexual spore. 10.

Zygomorphic : applied to a flower in which the parts in one or more sets are not similar ; irregular. 229.

Zygote : the sexual spore resulting from conjugation. 15.

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